BEHAVIORAL THERMOREGULATION IN ANISOPTERA

By

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BEHAVIORAL THERMOREGULATION IN ANISOPTERA

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Several species of Anisoptera maintain their body temperature more constant than ambient temperature. Species that spend most of their active period on perches and make only short flights (perchers) thermoregulate heliothermically, primarily by means of postural adjustments and perch site selection. Even the smallest species probably obtain some thermal advantage from postural adjustments. Some of the species that fly continuously (fliers) are endothermic regulators during flight. They regulate body temperature largely by: 1) controlling metabolic heat production by alternately using gliding or powered flight; 2) controlling heat loss by altering circulation between the thorax and abdomen. Small fliers are unable to regulate well because they are subject to high rates of convective heat loss.

Cooling constants, as defined by Newton's law of cooling, are related to thoracic weight by a negative power function over a wide size range. Cooling constants were higher in live dragonflies than in dead ones, a difference that was accentuated at high ambient

temperatures. The high cooling constants probably result from increased rates of circulation at high temperatures.

Most fliers, and some large perchers, are able to elevate their body temperature endothermically by "wing-whirring." In some species the rate of heat production apparently varies in response to ambient temperature. The body temperature at which flight is initiated after warm-up is positively correlated with body weight. This is probably because wing loading increases with increasing body size. Warm-up rate is positively correlated with thoracic weight up to weights of 0.5 g. This relationship may result from the weight dependence of metabolism and thermal conductance.

The maximum voluntarily tolerated body temperature and the threshold of heat torpor of several species were determined in laboratory and field studies. Both parameters are correlated with normal environment. The minimum temperature at which flight is possible is positively correlated with body weight and is higher in tropical dragonflies than in temperate zone species.

Body temperature is more variable relative to air temperature in tropical than in temperate zone species. The ability of dragonflies to maintain a relatively constant body temperature is determined primarily by climate, body size, and behavior.

Chairman

INTRODUCTION

Most of the so-called "cold-blooded" vertebrates thermoregulate, a view that began with the classical work of Cowles and Bogert (1944). Recently several workers have shown that this capability occurs in certain arthropods as well, especially insects in the orders Lepidoptera, Hymenoptera, and Homoptera (Cloudsley-Thompson, 1970).

Clench (1966), Heinrich (1972e), Kevan and Shorthouse (1970), and Vielmetter (1958) showed that some butterflies bask in the sun and orient themselves so as to optimize incident radiation. Watt (1968, 1969) showed in addition that color in butterflies is adaptively correlated with thermal environment. Heath and his co-workers (Heath, 1967; Heath and Wilkin, 1970; Heath *et al.*, 1971) have shown that cicadas may also regulate body temperature by basking and shade-seeking and that some types of their behavior occur only within narrow ranges of body temperature. During these studies Heath developed effective field techniques for measuring body temperature of large insects (Heath, 1967; Heath and Adams, 1969).

Not all insects depend on external heat sources to elevate their body temperature. Early work showed that a number of insects warm up before flight by rapid contractions of the wing muscles ("wing-whirring" or "wing-shivering"; Dotterweich, 1928; Krogh and Zeuthen, 1941; Dorsett, 1962). Adams and Heath (1964a, b) and Heath and Adams (1965, 1967) first showed true endothermic temperature regulation during flight and warm-up in sphinx moths. Hanegan and Heath (1970a, b, c) extended this work to the saturniid, *Hyalophora cecropia*, and Heinrich (1970a, b; 1971a, b) showed that the sphingid, *Manduca sexta*, controls circulation between the thorax and abdomen during flight. When ambient temperature is low there is little circulation between the tagmata and the heat generated by the flight muscles largely remains in the thorax, which is well insulated by scales. At low ambient temperatures thoracic temperature may exceed ambient temperature by as much as 30°C. When ambient temperature is high, however, circulation into the abdomen increases greatly, and much of the heat generated in the thorax is transferred to the poorly insulated abdomen, where it can be dissipated easily to the air.

Heinrich has also demonstrated well developed endothermy in bumblebees (1972a, b, c, d) and was able to relate the energetics of temperature regulation to pollination and reproductive behavior of the bees (see also Heinrich and Raven, 1972). Regulation of hive temperature in bees is well known (*e.g.*, Chapman, 1969; Cloudsley-Thompson, 1970).

Despite this growing literature, the number of insects known to thermoregulate is probably only a small fraction of those that actually do so. Most studies have been restricted to groups having fairly uniform responses to temperature. Thus, meaningful comparative studies are few, although Heath *et al.* (1971) drew some useful conclusions from a comparison of the extremely divergent strategies of cicadas and cecropia moths. Many questions leading to fruitful investigations of vertebrate thermoregulation have received little attention so far in work on insects. For example, what is the effect of body size on thermoregulation in insects? This parameter is very important in mammals (McNab, 1970), but, except for the recent papers of Bartholomew and Heinrich (1973) and Heinrich and Casey (1973), it has been practically ignored in insects. How are mechanisms of temperature regulation related to feeding and other behavior? To what extent is temperature response adapted to environmental conditions, and to what extent is it determined by morphology or evolutionary history? These and other issues deserve more investigation.

My purpose in the present work is to demonstrate thermoregulation in several species of dragonflies (Odonata, Anisoptera) and to compare the behavioral and physiological adaptations that make this possible in a number of different groups. I will present some data from all seven families of the suborder, mostly from members of the Libellulidae, Macromiidae, and Aeshnidae. The species comprise individuals ranging in body weight over about one and one-half orders of magnitude, in habitat from wooded streams to open fields, and in the climate they inhabit from warm temperate (Gainesville, Florida) to tropical (Panama Canal Zone). As a result of this study I can propose partial answers to the questions raised above, although final conclusions will, in many cases, require additional research.

Little previous work has been done on dragonflies. Corbet (1963) was the first to discuss at length the possibilities for thermoregulation in the order, and his ideas have been very fruitful in the present study, but he presented few quantitative data. Warm-up by wing-whirring was noted in Odonata long ago (Moore, 1953; Corbet, 1957), but has not been studied quantitatively. Hardy (1966) showed that in *Perithemis tenera* posture relative to the sun is correlated with air temperature, but he made no measurements of body temperature. Church (1960b) noted that the thoracic musculature of dragonflies is almost completely surrounded by superficial air sacs, and he showed that the air sacs substantially reduce heat loss from the thorax.

Adult dragonflies offer a number of advantages in a study of this kind. They are large and easy to observe in the field. Most species are readily distinguishable in the field. Although noted for their acrobatic flight, many species are reasonably easy to collect. They occupy a variety of habitats, and some species fly from dawn to dusk and from early spring to late fall in Florida, thus encountering a wide range of thermal conditions. They are diverse in size and some aspects of behavior, but are similar enough in general body form and basic biology that comparisons of body temperature, extent of thermoregulation, effect of body weight, and many other factors are meaningful.

MATERIALS AND METHODS

Animals

Adult anisoptera were collected in the vicinity of Gainesville, Florida, and in the Panama Canal Zone during the period April, 1971 - September, 1973. Table 1 lists the species used in this study (see also Table 8). The species for which I have extensive field and laboratory data, and which are the primary subjects of this thesis, are as follows: from Gainesville, *Anax junius* (Drury), *Erythemis simplicicollis* (Say), *Libellula auripennis* Burmeister, *L. needhami* Westfall, *Macromia taeniolata* Rambur, *Miathyria marcella* (Selys), *Pachydiplax longipennis* (Burmeister), and *Tramea carolina* (Linn.); from the Canal Zone, *Erythemis plebeja* (Burmeister), *Tauriphila argo* Hagen, *Tramea cophysa* Hagen and *T. walkeri* Whitehouse. Of these species, *Pachydiplax*, the two *Erythemis*, and the two *Libellula* are "perchers," as defined by Corbet (1963). They spend most of their active hours sitting on perches and intermittently make sallies to catch prey or interact with another dragonfly. The remaining species are "fliers," *i.e.* they remain on the wing almost constantly during their period of activity. Table 1 classifies as perchers or fliers the other species studied. All specimens were collected with ordinary aerial insect nets. All dragonflies used in laboratory studies were kept in metal boxes with moist paper toweling to prevent desiccation until use. Ordinarily insects were used within one day of capture, although on

Table 1. Species studied, with an indication of study site and basic activity pattern.

Species	Site	Activity Pattern
Petaluridae		
Tachopteryx thoreyi	Florida	percher
Cordulegastridae		
Cordulegaster sayi	Florida	percher?
Aeshnidae		
Anax junius	Florida	flier
A. longipes	Panama	flier
Coryphaeschna ingens	Florida	flier
C. perrensi	Panama	flier
Epiaeschna heros	Florida	flier
Gynacantha gracilis	Panama	flier
G. membranalis	Panama	flier
G. nervosa	Panama and Florida	flier
G. tibiata	Panama	flier
Nasiaeschna pentacantha	Florida	flier
Triacanthagyna caribbea	Panama	flier
T. dentata	Panama	flier
T. trifida	Florida	flier
Gomphidae		
Aphylla williamsoni	Florida	percher
Epigomphus quadracies	Panama	percher
Gomphus cavillaris	Florida	percher
G. dilatatus	Florida	percher
G. minutus	Florida	percher
G. pallidus	Florida	percher
G. plagiatus	Florida	flier?
Progomphus obscurus	Florida	percher
Macromiidae		
Didymops transversa	Florida	flier
Macromia taeniolata	Florida	flier
Corduliidae		
Epicordulia regina	Florida	flier
Somatochlora calverti	Florida	flier
Tetragoneuria cynosura	Florida	flier

Table 1 Continued

Species	Site	Activity Pattern
Libellulidae		
Erythemis credula	Panama	percher
E. plebeja	Panama	percher
E. simplicicollis	Florida	percher
Ladona deplanata	Florida	percher
Libellula auripennis	Florida	percher
L. needhami	Florida	percher
Miathyria marcella	Florida	flier
Micrathyria aequalis	Panama	percher
M. atra	Panama	percher
M. eximia	Panama	percher
M. ocellata	Panama	percher?
Orthemis ferruginea	Panama and Florida	percher
Pachydiplax longipennis	Florida	percher
Pantala flavescens	Florida	flier
Perithemis tenera	Florida	percher
Tauriphila argo	Panama	flier
Tramea carolina	Florida	flier
T. cophysa	Panama	flier
T. walkeri	Panama	flier

rare occasions as many as four or five days elapsed. The animals were not fed. Only mature individuals were used in both field and laboratory work, except for a few teneral specimens of *Anax*, as noted below.

Descriptions of collection sites around Gainesville appear in accounts of individual species. Most of the data on Panamanian dragonflies were obtained from species collected in the laboratory clearing of the Smithsonian Tropical Research Institute field station on Barro Colorado Island (BCI). Other species were taken in the forest on BCI or at two small, artificial ponds at Summit Gardens, a botanical garden in the Canal Zone.

Field Techniques

The procedure in field studies of body temperature was a modification of that used by Heath and his coworkers on cicadas (*e.g.*, Heath, 1967; Heath and Adams, 1969). Body temperatures were determined either with a Yellow Spring Instrument Co. hypodermic thermister probe, #524, equipped with a handle of balsa wood and polyethylene tubing, or with a hypodermic probe made following the design of Heath and Adams (1969) and using Veco #32A130 ultra small thermistors as the sensing element. Temperatures were read to the nearest 0.1°C on a YSI Telethermometer, Model 43TD. Each probe was calibrated in water against a laboratory mercury thermometer, and each was recalibrated at intervals of a few months. In one case a correction of 0.5°C was necessary after recalibration. In all others the correction was 0.2°C or less.

Each dragonfly was netted and quickly placed, still in the net, on a square of light colored styrofoam. The net was stretched tightly over its body and the probe inserted into the thorax. If the period from capture to measurement exceeded 10 seconds (estimated) or if I touched the insect, the reading was discarded. Generally insertion of the probe was lateral, but sometimes dorsal or even ventral insertion was necessary to obtain a reading within 10 seconds. The depth of insertion depended on the size of the insect. I made an effort to reach the approximate center of the thorax, but this necessarily involved some uncertainty.

The activity of each specimen was noted at the time of capture. In those that were perched the following were recorded: orientation relative to the sun and to the ground, position of wings relative to body, and in many cases, perch height and type of perch. Activities preceding capture were recorded if they seemed relevant to the thermal balance of an individual. The activity of flying dragonflies was not analyzed further unless they were engaged in some special behavior such as territorial patrol, sexual or aggressive encounters, or oviposition.

Ambient temperatures were measured with laboratory mercury thermometers. All were calibrated against a NBS calibrated Parr bomb calorimeter thermometer and were accurate to at least 0.5°C. In the field they were supported on a wooden rack 2-3 feet from the ground. One unaltered thermometer hung from the rack and was shaded by a piece of white cardboard. Two others had the bulbs painted with flat black paint and coated with carbon black. These were held with adjustable clamps and positioned so that their long axis was in a plane normal to the direction of the sun. One of these had the bulb partially shielded from wind by an aluminum tube painted flat black and closed except for a rectangular window permitting exposure of the bulb to the sun. The entire assembly was positioned in an exposed location within the collecting area.

Ambient temperatures were usually recorded at 15-30 minute intervals. In estimating ambient temperature at the time of each capture of a dragonfly, I assumed that ambient temperatures changed linearly between readings and that captures were evenly distributed in time between determinations of T_a. These assumptions probably have little effect on the accuracy of ambient temperature estimation during most of the day but should substantially improve accuracy during the early morning and late afternoon when air and black bulb temperatures were changing rapidly. On some occasions, particularly when working with large fliers like *Anax* and *Macromia*, the ambient temperatures were noted immediately after each capture, since intervals between captures were generally long. Occasionally, air temperature was measured at the site of capture with the hypodermic probe. In these instances I tried to insure equilibration of the probe by waving it in the air for 30-60 seconds after reading. Other weather conditions were noted as seemed appropriate but were not quantified. Cloud cover was rated on a subjective scale of 1 (very light haze) to 5 (dark clouds completely obscuring sun).

To measure body temperatures at equilibrium in the shade or in the full sun, animals were tethered by metal clips with the wings over the back, and suspended from the thermometer rack. The long axis of the body of the exposed specimen was oriented approximately normal to the rays of the sun. These controls were run only for perchers, since it seemed that little could be learned from tethered fliers, which do not bask.

Several sources of error are inherent in these methods. First, since the animals are quite small, the initial temperature of the probe might affect the reading. Heath and Wilkin (1970) found that this was not true for their probes used on cicadas. However, the smallest dragonfly studied here, *Pachydiplax*, has a thorax about 1/3 the mass of that of cicadas, and the commercially manufactured probes used initially may have a substantially higher heat capacity than Heath's probe. Therefore the effect of one of these probes was tested on tethered specimens of *Pachydiplax*. Temperatures were simultaneously determined in the field under varying exposures to solar radiation by implanted copper-constantan (Cu-Cn) thermocouples, read on a Thermo-Electric Mini-Mite thermocouple reader, and by the thermister probe. These sets of temperatures were related by a linear regression, the equation for which was $T_r = 1.02\ T_t - 0.1$, where T_r is the probe reading and T_t the thermocouple reading. The readings are not significantly different, although the probe tends to give a slightly higher reading, presumably because it warmed when exposed to the sun. This error appears to be unimportant, although as an added precaution I took care not to leave the probe on or near the ground exposed to the sun.

A second potentially important threat to the accuracy of body temperature measurements is the possibility that body temperature might change between the time of capture and the time of measurement. Since there was usually a substantial differential between air and body temperature there must indeed have been some change in body temperature. Heath and Adams (1969) and Heath and Wilkin (1970) specifically cautioned that the time interval between capture and measurement should be limited to 5 seconds. Working alone with such agile insects as dragonflies I found that this was impracticable, but as already mentioned, a 10 second limit was maintained. Captured insects were also kept out of the direct sun, so the greatest differential to which they were exposed was between body and shade temperature. In *Pachydiplax* this difference was maximally about 15°C. The cooling constant (see p. 119) of this species is generally between 0.4/min and 0.5/min, meaning that if $T_b - T_a = 15°C$, T_b should drop not more than 1.25°C in 10 seconds. In fact, there was probably even less error than this in most cases, since this calculation assumes the extremes of temperature differential and conductance. In addition, the probe was often left in place for more than 10 seconds after initial insertion, and a change of more than a few tenths of a degree was never observed. Thus, it is probably reasonable to assume that for *Pachydiplax* the measured body temperature was within 1°C of the true temperature in the great majority of cases. The error should be no greater in the other species studied since they are all at least as large. It may be noted that this type of error should tend to obscure thermoregulation if it occurs, since the greatest values of $T_b - T_a$ occur at low T_a, thus reducing apparent T_b more at low than at high values of T_a.

Another way in which T_b might be altered is by heat exchange with the experimenter. Heath and Wilkin (1970) emphasize that they kept their hands at least 10 cm from their animals. Again this proved impracticable for me. However, in laboratory tests, the body temperature of a *Pachydiplax* changed no more than a few tenths of a degree in 10 seconds when my hand was only 2-3 cm from it, although T_b rose rapidly if the thorax was actually touched.

Finally, if the specimen struggled in the net after capture it could raise its temperature by internal heat production. The fastest rate of warm-up ever observed in laboratory studies was about 8°C/minute, indicating a maximum elevation of 1.3°C in ten seconds. Since fast warm-up rates were seen only in fliers, which normally already were producing heat rapidly in flight when collected, there usually was probably much less elevation of temperature.

Determination of Minimum Flight Temperature

The minimum temperature at which level flight can be sustained was determined for the species listed in Table 2 by the method of Heath and Adams (1969). Specimens were cooled in a refrigerator, then repeatedly tossed into the air until they could maintain level flight for several feet. Then they were quickly netted and body temperature was measured with the thermistor probe already described. Each individual was released at room temperature before cooling to ascertain that it could fly at that temperature. No individuals with broken wings or other injuries were used.

Some specimens became disoriented or were injured if cooled too rapidly or taken to too low a body temperature, so that they failed to fly even at room temperature. For that reason specimens were only cooled a few minutes. If they could fly immediately, they were replaced and cooled a little longer.

Determination of Upper Limits of Tolerance

The body temperature of dragonflies was continuously monitored with fine wire Cu-Cn thermocouples to study the upper limits of tolerance. The wire, obtained from Omega Engineering, Inc., was either 0.003" diameter, Teflon insulated, or 0.002" diameter, uninsulated. The latter was coated either with Insul-X lacquer or fingernail polish before use. Thermocouple junctions were made by twisting the wires together and melting the tips in a Bunsen burner until a small bead formed. Readout was either continuously recorded on a Honeywell Electronik 19 two-channel chart recorder, or in the case of species studied in Panama, recorded by hand from a Thermo Electric Mini-Mite thermocouple reader. The thermocouple leads were connected to the chart recorder through a Con-Ohmic thermocouple reference junction; output could be read to 0.1°C with the recorder and to 0.5°C with the Mini-Mite. Each junction was calibrated against a mercury thermometer, often at several different temperatures. Except in rare cases the departure from the nominal value of 40 µv/°C (Weast, 1966-1967) was insignificant over a range of 20-30°C. At most it amounted to 0.5°C. The thermocouple readings of water bath temperatures were stable and reproducible to 0.1°C over at least five hours when the chart recorder was used.

The experiments in Gainesville were performed in a Lab-Line Constant Temperature Room in which temperatures could be varied from

0-60°C. At a given setting temperature fluctuated sinusoidally with an amplitude of about 1°C and a period of 1-3 minutes. At 15°C, the coolest temperature normally used, the room temperature was elevated about 0.4-0.5°C when the investigator was in the room. Relative humidity was uncontrolled and varied from 20-60% on occasions when it was measured. Air velocity near the insect was less than 0.25 m/second.

No such facility was available in the Canal Zone. Experiments there were performed in an air conditioned laboratory at 25 ± 1°C. Temperature was held within this range by adjusting the air conditioner and judiciously selecting time of day when this temperature was easily attained.

The junction was implanted to a depth of 1-5 mm in the thorax through a pinhole in the left metepisternum. The depth of insertion depended on the size of the dragonfly. Dissection of several specimens revealed that this mode of insertion left the junction within the mass of flight muscles, usually in the metathorax. The junction was held in place either with a drop of beeswax-paraffin mixture or with a small amount of Elmer's contact cement. No anesthesia was used.

After an animal had recovered from the implantation, it was released from restraint and placed on a vertical stick. It usually hung quietly while being heated with a 250 W heat lamp at 1-4°C/minute. At some point the insects avoided further heating, either by moving to the shaded side of the stick, assuming special postures, or flying away. The body temperatures at which these behaviors occurred were noted. Then the animal was restrained in the light and heated at rates of 1-7°C/minute (usually 1-4°C/minute). The point at which motor control was lost was also noted. Heating was then discontinued and the animals invariably recovered after cooling.

The principal causes of error in the measurement of upper temperature tolerance lie in the difficulty of deciding whether avoidance or paralysis had occurred and whether the dragonfly had been disturbed. These are related problems. Avoidance reactions were usually obvious and the associated body temperature could be determined to within 0.5°C, except when the animal flew off the stick. Because flight could have been caused by disturbing the specimen, avoidance was scored in these cases only if the animal, after being cooled a little and replaced on the stick, flew again at a T_b within 2°C of the temperature of its previous flight. The mean T_b was taken as the point of avoidance.

Recognition of paralysis was often more difficult. With continued heating, three phases of response could often be discerned: coordinated struggling, vigorous movement with progressive loss of coordination, and feeble, uncoordinated movements. I tried to record the beginning of the last phase as the point of paralysis. Individual determinations might on occasion be inaccurate by as much as 2°C, but normally the accuracy was probably within 1°C. Since I had to be close enough to watch both the dragonfly and the record of T_b rather carefully, no attempt was made to conceal myself from the insect. However, all unnecessary and sudden movements were avoided.

Investigation of Warm-Up and Conductance

In measuring these parameters the techniques of environmental control and temperature recording described above were used. After implantation of a thermocouple a specimen was allowed to cool, if its temperature was above ambient as a result of its struggling, to within 1°C of ambient. Then the wings were freed and it was placed on a vertical stick. If wing vibration did not begin spontaneously, I pinched the end of the abdomen gently with forceps and repeated this stimulation for up to 10 minutes. If no warm-up behavior was initiated within this period, this was noted and stimulation discontinued. If the animal began to warm up by wing-whirring it was permitted to continue undisturbed until takeoff. If it stopped without taking off, it was pinched again until it either began to warm up again or flew off the perch. In the latter event, takeoff was not considered spontaneous and the associated T_b was not used to characterize the temperature of spontaneous flight. Warm-up rate was determined by measuring the maximum slope of the trace of T_b vs. time. In most cases warm-up was virtually linear with time throughout most of its course (see pp. 149-150).

After warm-up the specimen was placed on a wooden perch in a metal box or glass desiccator in the dark and allowed to cool. Usually relative humidity was maintained at near 100% with wet paper toweling or distilled water in the well of the desiccator. In a few cases relative humidity was lowered to near 0% with Drierite or silica gel. Thermal conductance was calculated from the cooling curves by the method of Heath and Adams (1969). In the analysis it is assumed that the change in body temperature follows Newton's law of cooling, *i.e.*, $dT_b/dt = K(T_b - T_a)$, where K is the cooling constant. Thus a plot of $\Delta T_b/\Delta t$ vs. $T_b - T_a$ has a slope approximately equal to the cooling constant. Points were selected from the continuous record at one minute intervals, beginning only after the dragonfly had cooled several degrees. Since recording apparatus was not available in Panama, cooling curves were determined by timing with a stopwatch one to four degree decrements of body temperature. Calculations were essentially the same except that time intervals were unequal.

In instances where the dragonfly would not warm up by shivering, or where it warmed too little to obtain a good cooling curve, it was placed in a pasteboard box under a 250 W lamp and heated to at least 10°C above ambient. It was then allowed to cool as already described. When cooling constants of dead specimens were determined, they too were heated in this way.

Several authors (Krogh, 1948; Heinrich, 1971a) have pointed out that significant heat may be lost from insects through the leads of implanted thermocouples, reducing the rate of warm-up and increasing the rate of cooling. The possibility was tested in two ways on specimens of *Pachydiplax* and *Perithemis tenera*. First cooling curves were run on dead individuals with one and then two sets of 0.002" diameter leads implanted. No increase in cooling rate was apparent with two sets. Second, a living specimen of *Pachydiplax* with leads implanted was positioned approximately 1 cm above an ice water bath. When its body temperature had become stable, the leads were plunged into the bath to within 1 cm of the insect's thorax. No change in body temperature was noted over a five minute period. The 0.003" diameter leads were not tested in this way, but since they were insulated and were used only on species larger than *Pachydiplax*, it seems unlikely that they had any greater effect. I always remained at least several decimeters from the specimen except during implantation and brief periods of stimulation to prevent heat transfer from myself to the specimen.

Newton's law of cooling describes temperature change in a body with a uniformly warm core surrounded by an insulating shell of zero heat capacity. This model may apply when warm-up is endogenous. However, when an object is warmed from the outside, then cooled, the surface will initially be warmer than the core. For this reason all specimens were permitted to cool a few degrees to reverse the temperature gradient before using the data for calculation of conductance. In any case, almost all plots of $\Delta T_b/\Delta t$ vs. $T_b - T_c$ gave fairly good straight lines extrapolating near zero, so the slopes gave an adequate index to cooling rates.

Other aspects of thermal conductance in *Anax* received some attention. A series of experiments investigated the relation of cooling constant to air speed. Dead specimens of *Anax* were suspended with the wings held vertically over the back in a wind tunnel. The tunnel had a closed working section of 52 cm X 20 cm X 20 cm and was equipped with an entrance cone and baffles. The air stream was produced by a centrifugal fan driven by a belt and pulley system from an electric motor. Air speed, which varied between 0 and 3.9 m/second, was determined for each pully combination with a Biram's type anemometer. Specimens were heated directly with a lamp and quickly placed in a tunnel, where cooling curves were obtained in the usual way. T_a was not strictly controlled but normally was about 25°C.

Another group of experiments was intended to elucidate the possible effect on thermal conductance of the thorax of circulation of haemolymph from the thorax to the abdomen. Living specimens of *Anax* were prepared as described above except that a thermocouple was implanted laterally in the abdomen, usually in the second or third segment, as well as in the thorax. These specimens were heated with a lamp to 10-15°C above ambient. Cooling curves for both the thorax and the abdomen were measured on each individual at ambient temperatures of 15 and 35°C. Then a clamp, made of two narrow spring metal strips held together at each end by short lengths of plastic tubing, was fastened tightly across the first abdominal segment, and determinations were repeated at the same ambient temperatures. Finally, the clamp was removed, the specimen killed in KCN, and the cooling curves repeated again. Cooling constants of both thorax and abdomen were calculated as usual.

The possibility that contact with the metal clamp accelerated cooling cannot altogether be discounted, but this effect should not depend on ambient temperature so any difference between conductance at 15 and 35°C should be due to other causes. The same may be said for possible injury to the abdomen by the clamp or the thermocouple.

Local Heating Experiments

Thoracic and abdominal temperatures were simultaneously monitored in living *Anax*. The insects were immobilized on an insect spreading board by holding down their wings with lead weights. The abdomen was shaded by a small piece of aluminum foil fastened to a cork. A microscope light, which could be focused on an area of less than 1 cm^2, was shone on the thoracic dorsum so that the thorax was rapidly heated. This was repeated at several air temperatures. Near the end of some experiments, while the thorax was held at an elevated temperature, the base of the thorax was pinched with forceps, so that most circulation between thorax and abdomen was cut off. After a few minutes the abdomen was released and body temperature measurements were continued for several more minutes

Investigation of Role of Wing Position

The influence of variations in wing positions on body temperature in *Pachydiplax* was investigated as follows. An incadescent lamp was fixed on an arm that could be rotated about a fixed bolt and clamp through approximately 180° in a vertical plane. The angle of the arm was determined with a carefully handmade cardboard protractor centered on the axis of rotation. A dead specimen of *Pachydiplax* was mounted with contact cement on a thin wooden dowel and positioned at the center of rotation with its long axis parallel to the axis of rotation. Thoracic temperature was monitored with an implanted thermocouple. The wings were positioned either in a horizontal plane or pushed forward and well below the horizontal. Each specimen was run at both wing positions. These positions approximate natural positions often seen in the field (p. 30). The wings were held in place by small spots of contact cement. As little cement as possible was used to prevent any shading of the thorax by the opaque glue. Equilibrium thoracic temperature was recorded for several different light angles at each wing position.

In addition to possible effects of the glue, the possibility exists that the position of the thorax was not exactly the same relative to the light during runs at the different wing positions. Secondly, at times it was difficult to position the wings in a completely natural and symmetrical way, and at times they shifted positions slightly as the glue contracted. Since several replications were made, these errors should have no consistent overall effect.

PATTERNS OF THERMOREGULATION

This section presents an overall picture of thermoregulation in each species that was investigated extensively. The following accounts are based primarily on field data but results from laboratory experiments supplement the analyses.

Pachydiplax longipennis

As long ago as 1899 Williamson remarked on the peculiar posture that *Pachydiplax* sometime adopts, with the abdomen pointed almost straight up (Figures 1A and 2A). Corbet (1963) speculated that a similar posture, which he described as an "obelisk," in certain tropical species might serve a thermoregulatory function by minimizing the surface area intercepting radiant energy. Although elevation of the abdomen in *Pachydiplax* may have more than one significance, it clearly reduces the radiant heat load in many cases.

Figure 3 is a plot of T_b vs. T_a in this species. Specimens were collected primarily at breeding sites, at small, sunny ponds and ditches, but many were also taken in open areas away from the water. This figure excludes all teneral specimens and those adults to which sun was not available, since this species is heliothermic, as will be shown shortly. They may remain active in the absence of sun, however, especially in warm weather.

Perhaps the most striking feature of Figure 3 is the correlation of certain postures with particular ranges of T_b. Some of the postures

Figure 1A. Male *Pachydiplax longipennis* in obelisk posture.

Figure 1B. Male *Pachydiplax* oriented perpendicular to the sun with wings in the "down and forward" position; sun is above the plane of the paper and slightly to the viewer's right.

Figure 2A-B. Body positions in *Pachydiplax* that minimize exposure to the sun. Wings not shown.

Figure 2C-E. Body positions that maximize exposure to the sun; stippling indicate sun above or behind plane of paper (modified from Hardy, 1966).

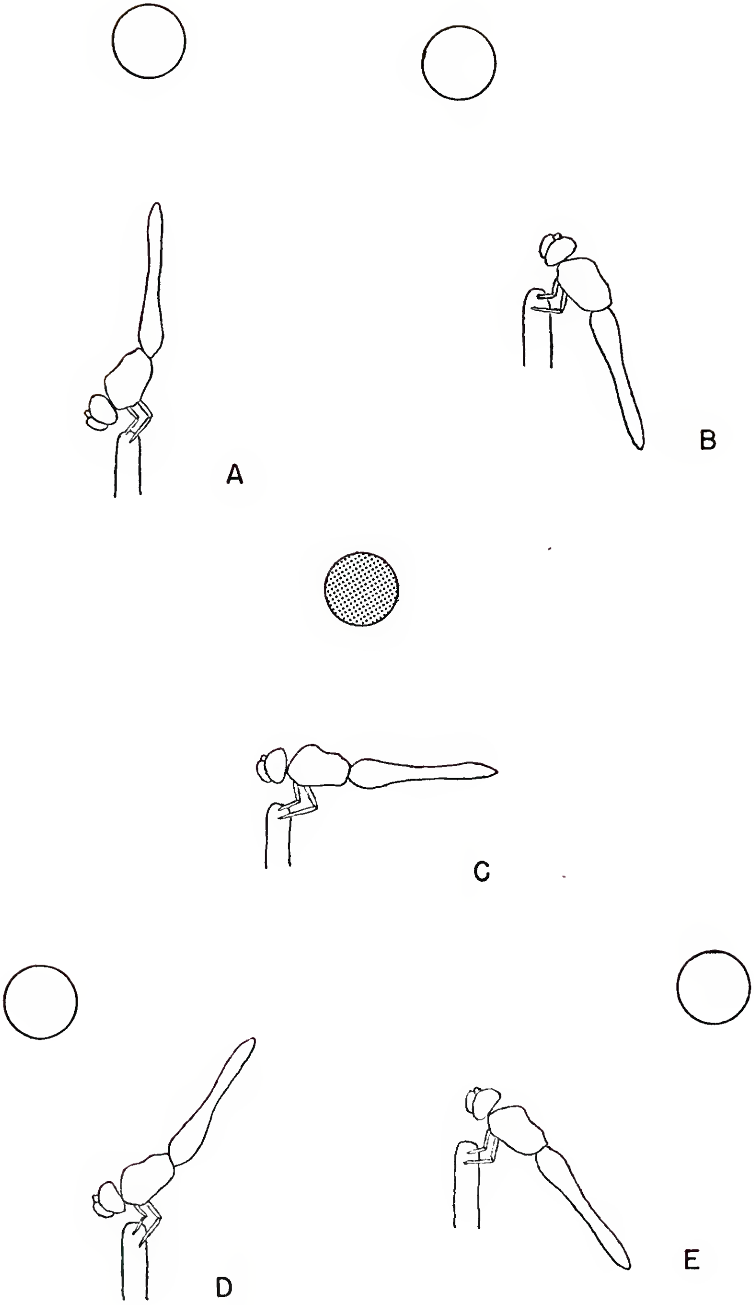
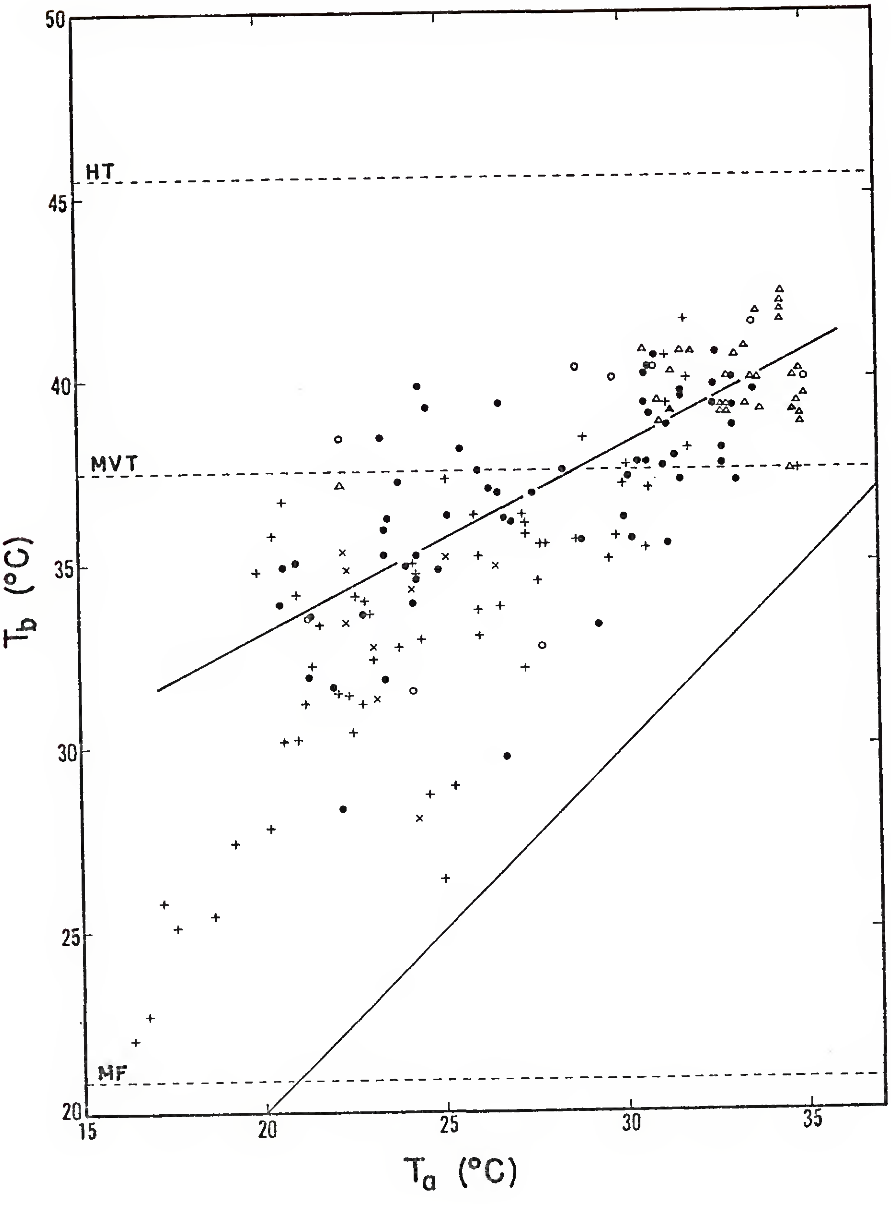

A
B
C
D
E

Figure 3. Relation of T_b to T_a in free-ranging *Pachydiplax*. Thin straight line indicates line of thermal equality, dashed lines the levels of critical temperature as determined in the laboratory (HT - heat torpor, MVT - maximum voluntary tolerance, MF - minimum flight temperature), and the heavy line the linear regression of T_b on T_a of specimens above the lower limit of the preferred range of T_b (see text). Each point represents one field measurement, and postures are indicated as follows: + - perpendicular to sun, X - other postures maximizing radiant heating, Δ - obelisk, ▲ - other postures minimizing radiant heating, • - all other perched specimens, ◦ - specimens in flight.


50
45
40
35
30
25
20
HT
MVT
MF
15
20
25
30
35
T_b (°C)
T_a (°C)

involved are shown in Figures 1 and 2. Those that appear to reduce the surface area exposed to the sun are the obelisk, already mentioned, and that shown in Figure 2B, in which the individual faces the sun with the abdomen and thorax depressed. In a variation of the obelisk, which may occur during times when the sun azimuth is relatively low but the heat load is still high, the specimen faces away from the sun with the abdomen partially elevated and pointing directly at the sun. Of these postures, the typical obelisk is the most common. In the most common posture that appears to maximize solar heat input, the insect perched horizontally with the long axis of the body normal to the horizontal direction of the sun's rays (referred to as the perpendicular position; Figures 1B and 2C). Less common positions placed the specimen facing the sun with the thorax and abdomen elevated, or facing away from the sun with the abdomen and thorax depressed (Figures 2D and E respectively).

Figure 4 presents the frequency distribution of postures of perched specimens as a function of T_b and T_a. It is clear that the obelisk and other positions that could reduce solar input occur only when T_b is high and at very high T_b are the only perching postures observed. Postures that presumably increase solar input are the only ones observed below T_b of about 30°C, but they are also seen at intermediate and high T_b. However, it appears that postures are more closely related to T_b than to T_a.

Figure 5 shows that wing position is also strongly correlated with T_b. Three wing positions were recognized. In the "down and forward" position the wings were held below the plane of the thoracic terga and were skewed cephalad (Figure 1B). The degree of depression

Figure 4A. Frequency distribution of postures as a function of T_b in *Pachydiplax*. Symbols are as follows: ■ - perpendicular posture, □ - other postures maximizing exposure to radiant heating, ▧ - neutral postures, ▨ - obelisk, ▦ - other postures minimizing radiant heating.

Figure 4B. Posture as a function of T_a in *Pachydiplax*, otherwise as in A.

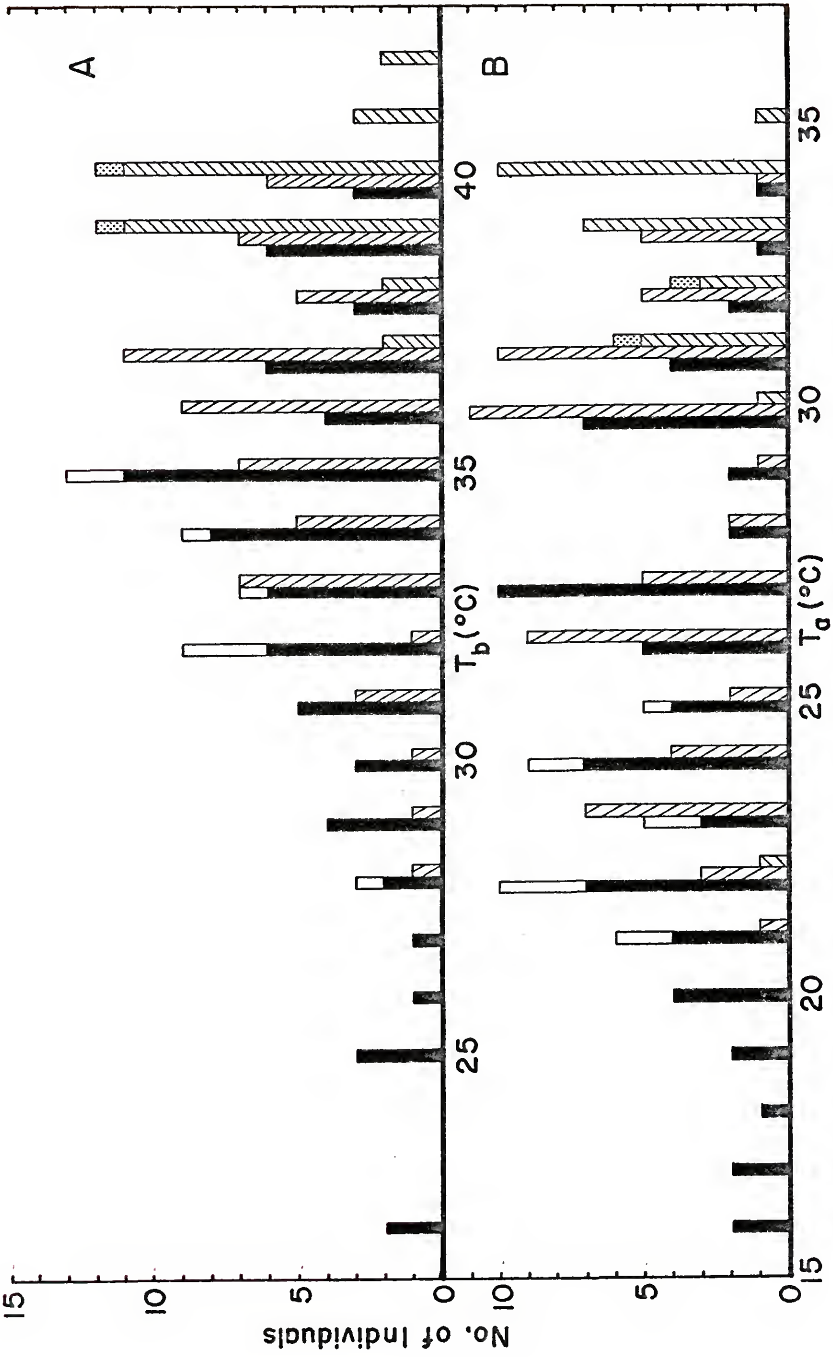
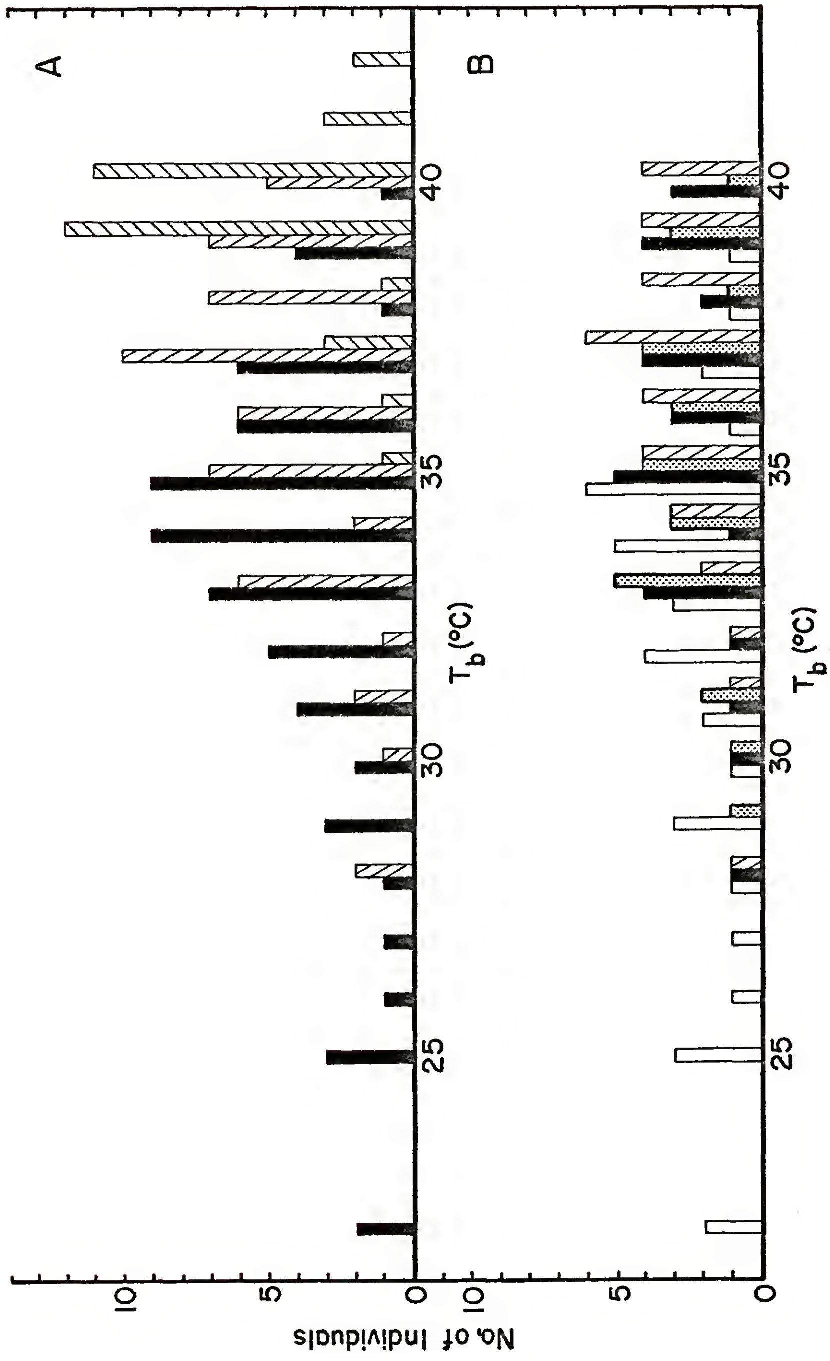

A
B
No. of Individuals
15
10
5
0
10
5
0
T_b (°C)
25
30
35
40
T_a (°C)
15
20
25
30
35

Figure 5A. Frequency distribution of wing position as a function of T_b in *Pachydiplax*. Symbols are as follows: ■ - wings in the down and forward position, ▧ - wings held flat, ▨ - wings elevated above the plane of the terga.

Figure 5B. Frequency distribution of certain posture and wing position combinations in *Pachydiplax*. Symbols are as follows: □ - perpendicular posture, wings down and forward; ■ - perpendicular posture, wings flat or elevated; ▦ - neutral posture, wings down and forward; ▧ - neutral posture, wings flat or elevated.


A
B
No. of Individuals
0
5
10
0
5
10
25
30
35
40
25
30
35
40
T_b (°C)
T_b (°C)

and promotion varied greatly and this position sometimes was indistinguishable from the "flat" position. In the "elevated" position the insect raised its wings well above the plane of the terga, as in Figure 1A. Clearly there is a tendency to hold the wings down and forward at low T_b and elevated at high T_b. These wing positions are associated with certain postures (Table 2), but the down and forward position, at least, is independently correlated with low T_b. Figure 5B shows that individuals perched perpendicular with wings down and forward have lower body temperatures than those perched perpendicular with wings flat or elevated. Individuals perched parallel to the sun's rays, or in an intermediate position, are less likely to have the wings down and forward if T_b is high. In addition, when dead specimens with their wings positioned down and forward were heated with a lamp, they tended to equilibrate at higher T_b than specimens with wings in the flat position, except when the lamp was exactly horizontal (Table 3). In nature, dragonflies would seldom encounter a situation where incident sunlight came in exactly a horizontal direction, because the true horizon is normally obscured by vegetation or slight elevations of land. The elevated wing position may decrease heat load in itself, but it may also simply assist in maintaining balance in the obelisk posture.

Two aspects of the results are in apparent disagreement with the conclusions of others. Johnson (1962b) showed that the bluish-white pruinescence on the abdominal dorsum in mature male *Pachydiplax* serves as a sexual recognition signal, and he noted that in males of this species the abdomen is often raised. He concluded that these

Table 2. Frequency of various posture and wing position combinations in *Pachydiplax*.

	wing position		
Posture relative to sun	down	flat	up
Perpendicular	38	26	2
Intermediate	17	15	1
Parallel	12	14	2
Obelisk	0	2	29

Table 3. Effect of wing position on equilibrium T_b in dead *Pachydiplax*. Absolute values of $T_b - T_a$ ranged from 5 - 28°C.

Lamp Position (degrees above horizontal)	N	n[a]	$\overline{\Delta T}$ (°C)[b]
0	10	5	- 0.34
30	10	10	1.63
60	9	8	1.24
90	9	8	1.42

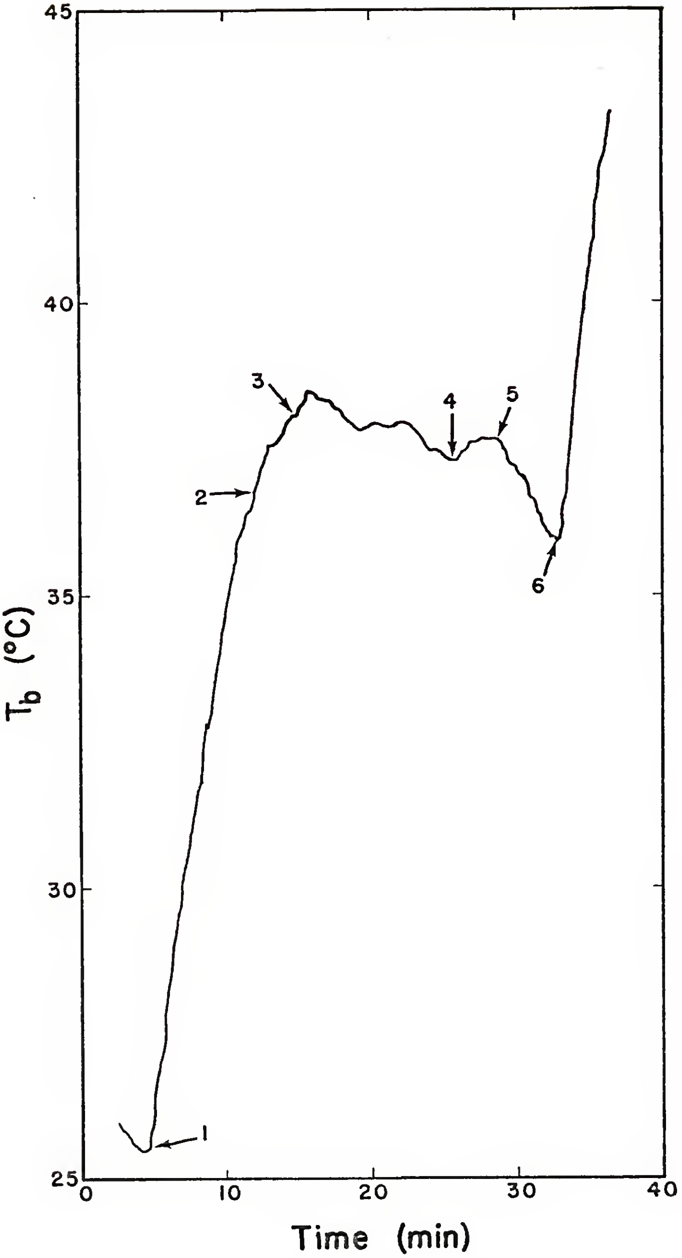
[a] number of specimens in which equilibrium T_b was higher with wings depressed.

[b] mean difference between equilibrium T_b with wings depressed and T_b with wings flat.

dragonflies elevate their abdomen in order to display the white signal. Male *Pachydiplax* often raise their abdomen during aggressive encounters with other males, especially when they meet in flight or when a male on a favorite perch is approached by a flying male. Also, many dragonflies raise and curl their abdomen when touched or approached, particularly if tethered in the laboratory or otherwise prevented from flying. On one or two occasions a *Pachydiplax* in the field was seen to abruptly raise its abdomen when approached. Nevertheless, the function of the raised abdomen is often thermoregulatory as is shown by the fact that the obelisk posture is always associated with a high T_b. Furthermore, the position is often assumed by females and by males away from breeding sites. Also, if an individual in an obelisk is shaded, *e.g.* by a cloud or an insect net, it will lower its abdomen to a horizontal position. When the shade is removed, it resumes the obelisk in a series of jerky movements. I have repeated this observation many times without any exceptions to this pattern. Finally, individuals heated with a lamp in the laboratory will often assume an obelisk or equivalent posture at high T_b. If they are perched on the side of a vertical support and the lamp is directly behind rather than above them, they will assume a posture that looks identical to the typical obelisk except that it is rotated 90° in a vertical plane. The abdomen of the insect still points almost directly at the light. This action is in fact effective in preventing or slowing further rise of T_b (Figure 6).

The second point of controversy concerns wing position. Several authors have suggested that dragonflies lower their wings at high

Figure 6. A direct tracing from a recording of T_b in male *Pachydiplax* heated with a 250 W lamp, showing effect of obelisk posture. Arrows indicate the following sequence of events: 1) lamp turned on, 2) abdomen raised about 45°, 3) full obelisk, 4) specimen lowers abdomen and walks a short distance away from light, 5) full obelisk, 6) specimen in same location as 4) and 5) but with abdomen forced down to horizontal position.


45
40
35
30
25
T_b (°C)
0
10
20
30
40
Time (min)
1
2
3
4
5
6

temperature in order to shade their thorax (*e.g.*, Corbet, 1963). Johnson (1962b) and Paulson (1966) specifically associated wing depression with elevation of the abdomen in *Pachydiplax*. This suggestion seems reasonable *a priori*, and it receives support from Heath's (1967) observation that *Magicicada cassinix* can obtain some shading from its transparent wings. However, my data refute the idea in the present case. First, the distribution in Figure 5 clearly shows the connection of wing position and T_b; only once have I seen a *Pachydiplax* in a definite obelisk with depressed wings. This specimen was perched on an exposed twig in a gusty, shifting breeze. It depressed its wing when the wind blew from behind it and held them flat or elevated at other times. Second, lowered wings in dead specimens actually facilitate heating.

The reason for the disagreement is not clear. It may be that previous workers failed to distinguish functionally different postures. My data show a number of instances in which the wings were depressed and the abdomen slightly or moderately elevated. The mechanism by which lowering the wings permits higher T_b is also obscure. It may involve alteration of the thickness of the insulating air sacs surrounding the thorax.

It is now possible to draw the following picture of the behavioral responses of *Pachydiplax* to temperature under field conditions. At cool temperatures, particularly early and late in the day when the sun is visible but solar flux is low, these insects assume basking postures that maximize the amount of solar radiation intercepted. The most common posture is with the body horizontal and perpendicular to the sun's rays; the wings are down and forward. When T_b reaches the range of about 30-35°C, *Pachydiplax* begins to assume other postures, often without regard to their orientation relative to the sun. Many continue to use the perpendicular position, however, up to about 39°C, rarely 40-41°C. Above about 37°C postures that minimize radiant heating appear, and at higher temperatures they predominate.

It is interesting that *Pachydiplax* ordinarily does not seek shade to avoid overheating. On only two occasions were individuals apparently seeking shade, both when T_a exceeded 34°C. In one instance a female was hanging vertically in the shade of a twig and in the other a male perched beneath a layer of tall water hyacinth leaves. In both instances other individuals remained active in the sun. *Pachydiplax* may remain active at T_a as high as 37°C. Other individuals have been taken in the shade but not in association with particularly high temperatures.

One may now ask how effective are these behavior patterns in maintaining a constant T_b. Body temperatures occur outside of (most often below) the preferred range either because physical conditions are inappropriate or because T_b has not had time to reach an equilibrium. Most body temperatures resulting from these conditions should not be used in evaluating the precision of temperature regulation, because in all heliotherms T_b must vary from equal to T_a at night to some maximum value near midday.

To eliminate inappropriate values for T_b, those taken from basking individuals were not used. The solid line of Figure 3 represents a least squares linear regression through the remaining points. The regression equation is $T_b = 0.473\ T_a + 24.1$ (see Table 4). Such a regression measures two components of thermoregulation: the

Table 4. Statistics calculated from least squares linear regression of T_b on T_a in free-ranging Odonata.

Species	Sex	Mean Body Wt. (g)	Weight Interval (g)	N	a_1[a]	a_0[b]	r[c]	Syx[d]	Expected T_b at 20°C	35°C
Anax junius	--	1.038	--	42	0.402	27.4	0.831	1.29	35.4	41.5
	♂	0.993	--	20	0.496	24.5	0.924	0.98	34.4	41.9
	♀	1.071	--	22	0.296	29.9	0.527	1.40	35.8	40.3
Erythemis simplicicollis	--	0.270	--	90	0.425	26.3	0.780	1.72	34.8	41.2
	♂	0.231	--	23	0.500	24.4	0.873	1.40	34.4	39.9
	♀	0.285	--	66	0.429	26.2	0.782	1.67	35.0	41.2
	--	0.207	< 0.24	25	0.456	25.7	0.847	1.51	35.3	41.8
	--	0.266	0.24 - 0.29	30	0.489	24.5	0.794	1.90	39.7	41.4
	--	0.328	> 0.29	29	0.377	27.6	0.761	1.40	34.2	41.0
E. plebeja	♂	0.219	--	51	0.564	22.51	0.405	1.82	33.8	42.2
Libellula spp.	--	0.495	--	62	0.242	30.2	0.587	1.26	35.0	38.7
	♂	0.470	--	12	0.194	31.7	0.579	1.11	35.6	38.5
	♀	0.500	--	49	0.272	29.2	0.592	1.28	34.6	38.7
	--	0.416	≤ 0.46	16	0.114	33.2	0.228	1.47	35.5	37.6
	--	0.485	0.46 - 0.53	22	0.100	34.8	0.160	1.32	36.0	38.6
	--	0.579	≥ 0.53	19	0.259	29.4	0.593	1.43	34.2	38.7
Macromia taeniolata	♂	1.180	--	35	0.192	36.0	0.393	1.43	39.8	42.7
Miathyria marcella	--	0.160	--	34	0.782	13.0	0.803	1.67	28.6	40.4

Table 4 Continued

Species	Sex	Mean Body Wt. (g)	Weight Interval (g)	N	a_1[a]	a_o[b]	r[c]	Syx[d]	Expected T_b at 20°C	35°C
Pachydiplax longipennis	--	0.175	--	104	0.473	24.1	0.719	1.94	33.6	40.7
	♂	0.182	--	62	0.493	23.6	0.743	2.02	33.5	40.9
	♀	0.164	--	42	0.493	23.0	0.663	1.76	32.9	40.4
	--	0.126	$\leq$ 0.15	28	0.513	22.2	0.775	1.81	32.5	40.2
	--	0.173	0.15 - 0.20	35	0.427	25.6	0.709	1.58	33.3	39.8
	--	0.226	$\geq$ 0.20	24	0.576	21.1	0.786	1.85	32.6	41.3
Tauriphila argo	--	0.267	--	24	1.253	0.0	0.684	1.50	25.1	43.9
Tramea carolina[e]	--	0.360	--	44	0.681	18.3	0.863	1.26	31.9	42.1
T. cophysa and *T. walkeri*	--	0.334	--	33	0.782	15.6	0.707	0.92	31.2	42.1

[a] slope.

[b] Y intercept.

[c] correlation coefficient.

[d] standard error of estimate.

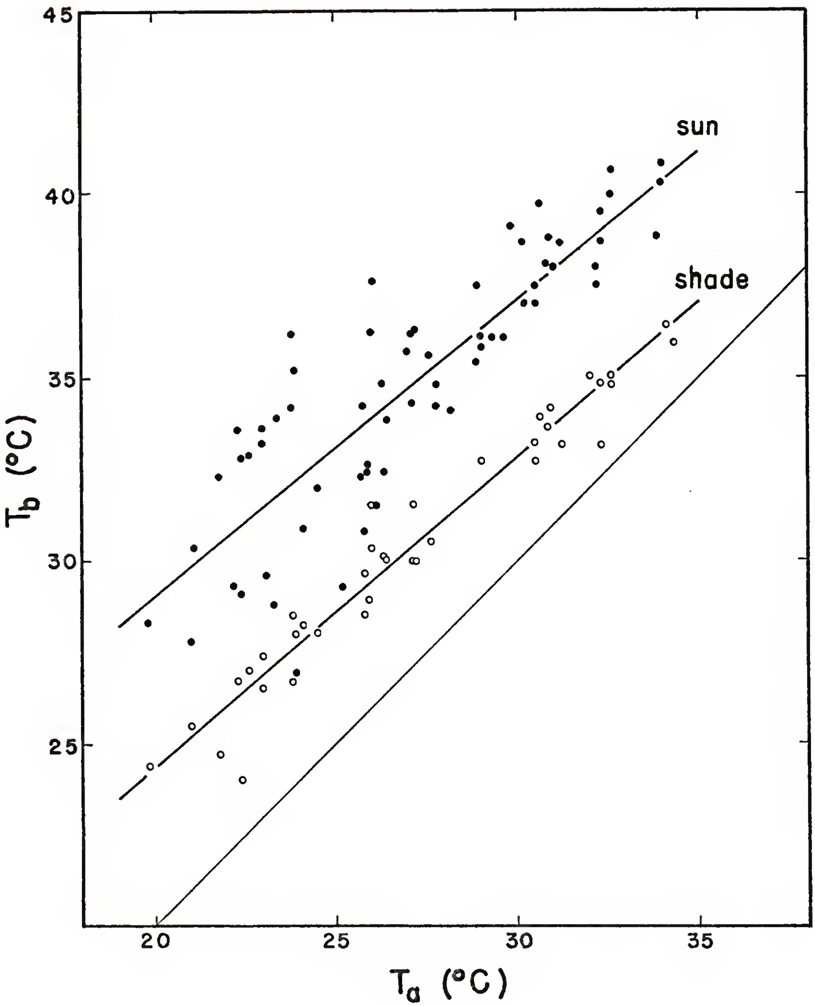
[e] based on specimens at T_a less than 32°C; see text and Figure 20.

regression coefficient represents the overall dependence of T_b on T_a and the standard error of estimate is a rough measure of the precision of regulation at any one T_a. These indices of thermoregulatory ability are analogous to those McNab (1970) used to describe thermoregulation in bats. They do not distinguish between variation of T_b resulting from imprecision in active temperature responses and variation due to the passive physical characteristics of the insects. Some other workers (*e.g.* Heath, 1965) define thermoregulatory ability of ectotherms primarily in terms of the precision of active responses. This aspect of thermoregulation will be discussed in a later section.

It is clear that in *Pachydiplax* T_b is, to a considerable extent, independent of T_a under favorable conditions. Figure 7 shows temperatures of specimens tethered in the sun or in the shade. In both cases the slope of the regression of T_b on T_a is significantly, although slightly, less than 1.0. Nevertheless, T_b obviously depends much more strongly on T_a than in free-ranging individuals. Evidently the latter do thermoregulate, and they must do so largely by varying posture and wing position, as suggested above. *Pachydiplax* can elevate T_b by endogenous heat production if forced to fly or struggle in the laboratory, but this seldom results in a temperature differential of more than 2-3°C. No evidence indicates that activity contributes to thermoregulation since these dragonflies are usually more active at high T_a. Table 4 reveals that the sexes regulate T_b equally well, despite the fact that males devote appreciable time to territorial defense.

All of the data discussed so far are from fully mature individuals (referred to hereafter simply as "adults"). Only a few data were

Figure 7. Relation of T_b and T_a in tethered *Pachydiplax*. Thin straight line indicates line of thermal equality, heavy lines the regression of T_b on T_a in exposed ($T_b = 0.81\ T_a + 12.84$) and shaded ($T_b = 0.84\ T_a + 7.65$) specimens.


45
40
35
30
25
T_b (°C)
20
25
30
35
T_a (°C)
sun
shade

obtained from teneral *Pachydiplax*, but the data available, coupled with those from other species, indicate that tenerals thermoregulate poorly and tend to have lower T_b than adults. The great majority of *Pachydiplax* found in deeply shaded areas are teneral. This is also true of the other libellulid perchers studied here. Adults only occasionally perch in full shade. This propensity of tenerals for shade and cool temperatures is probably related to the fact that their cuticle is incompletely hardened and therefore subject to excessive water loss.

In a few populations of *Pachydiplax*, both tenerals and adults seem to spend a large proportion of their time in the shade. At several of the large, cypress-bordered lakes in the Gainesville area, large concentrations of *Pachydiplax* breed among the emergent and floating vegetation under the cypresses, where only patches of sunlight are present. Therefore, the adults of these populations must often perch in the shade and consequently probably have lower or less well-regulated body temperatures than populations in more open areas. Of course, the former may experience a narrower range of ambient temperature. The ability of these groups to exist under what appear to be substantially different thermal conditions from most populations of the species emphasizes the facultative nature of thermoregulation in these insects. Such opportunism is characteristic of many aspects of the behavior of Odonata (Corbet, 1963; Paulson, 1966). Although *Pachydiplax* thermoregulates rather successfully in most situations, it is not prevented from colonizing areas where the opportunities for thermoregulation are apparently reduced.

Erythemis spp.

Erythemis simplicicollis is a small to medium sized (mean body weight - 0.270 g) libellulid, common in the Florida fauna. Most specimens were taken in an open field where there was no breeding activity. Figure 8 is a plot of T_b vs. T_a in this species. As with *Pachydiplax*, only mature specimens with sunlight available are plotted. Variations in perching posture are not shown in this figure, but their frequency is shown as a function of both T_b and T_a in Figure 9.

No individual in the genus *Erythemis* was seen to assume an obelisk posture. Species observed included *E. credula, haematogastra, peruviana, plebeja,* and *simplicicollis*. However, Needham and Westfall (1955) describe *E. peruviana* as perching with "flaming red abdomen erected and held steadily aloft, like a miniature obelisk." *Erythemis simplicicollis* rarely elevated its abdomen at all (three out of ninety-four observations in which abdominal orientation was scored).

Various other postures were observed in this species. In the perpendicular orientation *Erythemis* frequently holds its abdomen and thorax below the horizontal, thus probably reducing the surface area actually exposed to the sun. In a posture that more definitely indicates active basking *E. simplicicollis* exposes its dorsal surface to the sun by facing away from it with the abdomen and thorax horizontal or depressed. This posture is like that shown in Figure 2E for *Pachydiplax*, but it is rare in the latter species and common in *Erythemis*. The effectiveness of the posture is greatest when the insect is aligned exactly parallel to the angle of declination of the sun. The principal sun avoidance posture is essentially the mirror

Figure 8. Relation of T_b and T_a in free-ranging *Erythemis simplicicollis*. The thin broken lines connect points in chronological order. Open circles were not included in the calculation of the regression of T_b on T_a (see text). Other symbols as in Figure 3 except that postures are not differentiated.

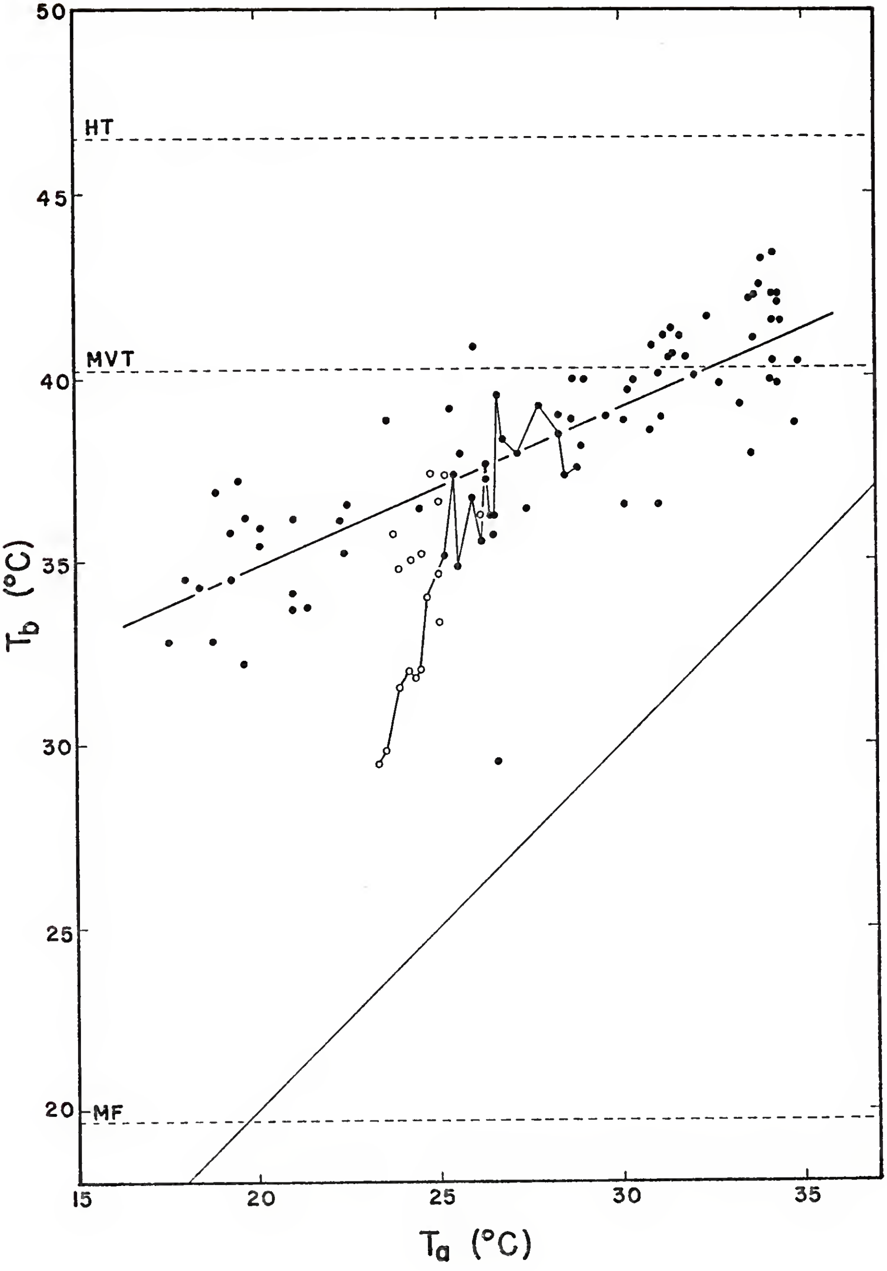

50
45
40
35
30
25
20
HT
MVT
MF
T_b (°C)
15
20
25
30
35
T_a (°C)

Figure 9A. Frequency distribution of posture as a function of T_b in *Erythemis simplicicollis*. Symbols are as follows: ■ - perpendicular posture; ▧ - postures in which specimens faced away from the sun, the long axis of the body parallel to the rays of the sun □ - as in previous class, but with the long axis of the body not parallel to the rays of the sun; ▨ - postures in which specimens faced toward the sun, the long axis of the body parallel to the rays of the sun; ▦ - as in previous class, but with the long axis of the body not parallel to the rays of the sun.

Figure 9B. Posture as a function of T_a in *E. simplicicollis*; otherwise as in A.

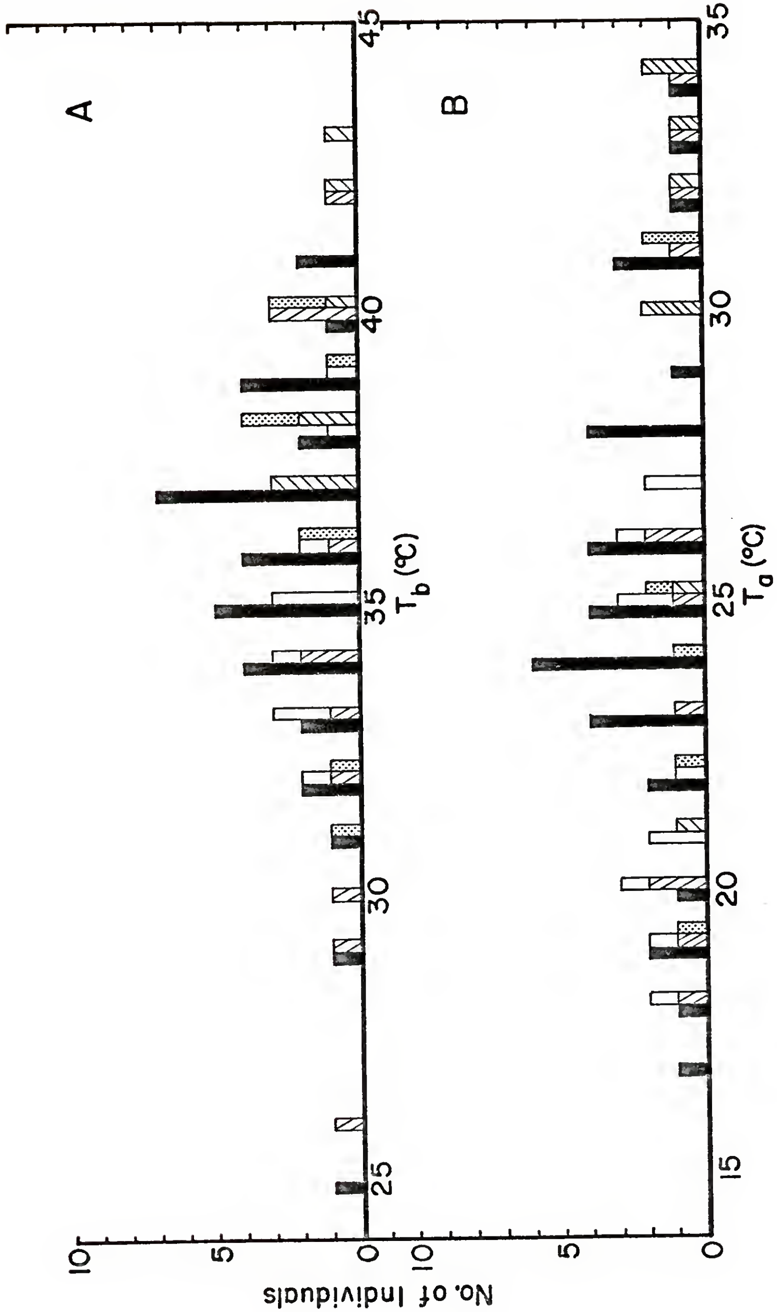

A
B
No. of Individuals
10
5
0
10
5
0
25
30
35
40
45
T_b (°C)
15
20
25
30
35
T_a (°C)

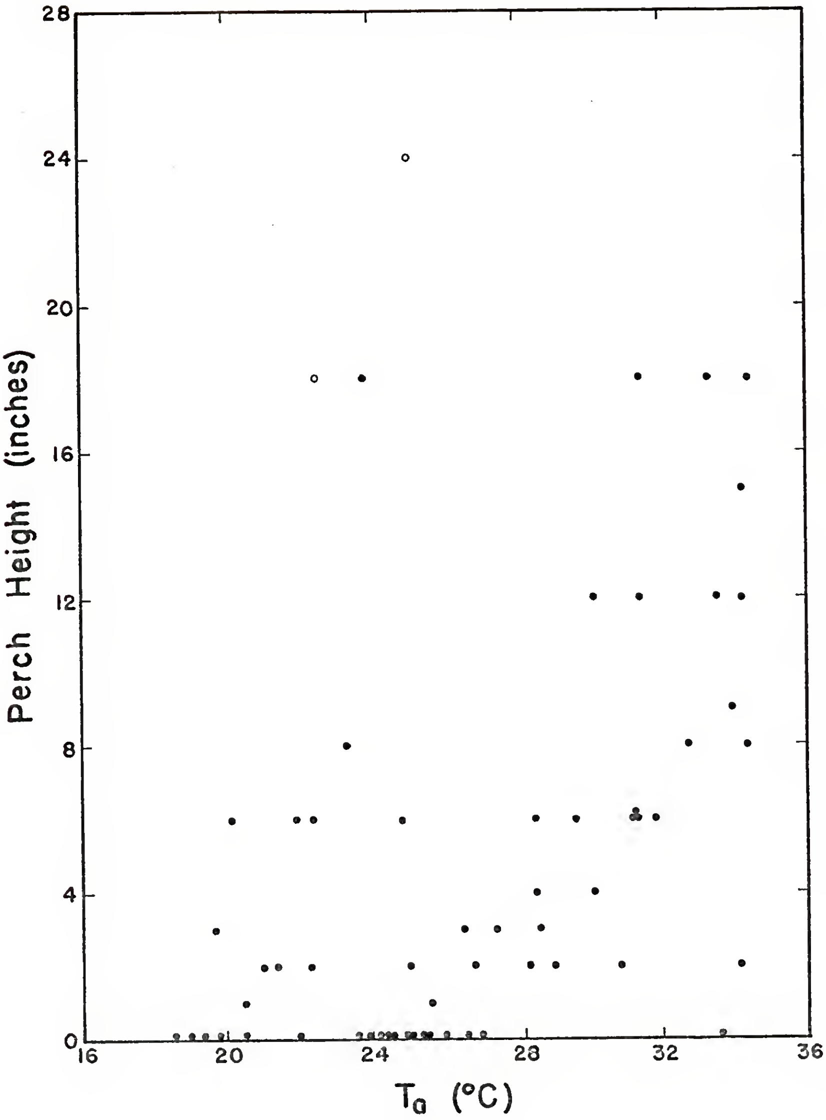
image of the one just described. Individuals face the sun more or less directly and depress the abdomen and thorax. This is similar to Figure 2B, except that *Erythemis* often perches on the side of a straight stem rather than at the top, so they may actually be partially shaded by the stem.

Figures 9A and B show that these postures correlate with temperature, as expected. Orientations that minimize radiant heat load are associated with high T_b regardless of T_a. The individual facing the sun with T_b in the interval 31-32°C was one of the rare specimens with an elevated abdomen. It probably was maximizing heat load (see Figure 2D). Postures that presumably maximize solar input are about as well correlated with low T_a as with low T_b, however.

Erythemis simplicicollis is somewhat unusual among the Libellulidae, although by no means unique, in that it frequently perches directly on or very near the ground. From shortly after sunrise until about sunset, ground surface temperatures are likely to be substantially higher than the temperature of the air a meter or two above ground (Lowry, 1969). Furthermore, there is little air movement at ground level, so heat loss by convection is reduced. Thus, *Erythemis* can, in effect, select a body temperature by perching an appropriate distance from the ground. Figure 10 suggests that they do this. *Erythemis* tends to perch at higher levels as T_a, measured in the usual way by a thermometer about two feet above ground, increases. The actual ambient temperature to which they are exposed tends to remain relatively constant.

Only one specimen was perched on the ground at T_a greater than 27°C. This individual was in a sun fleck in a generally shaded area and had a

Figure 10. Perch height as a function of T_a in *Erythemis simplicicollis*. Open circles represent individuals perched on broad, flat surfaces in the sun above the ground (see text). Elevations were estimated.

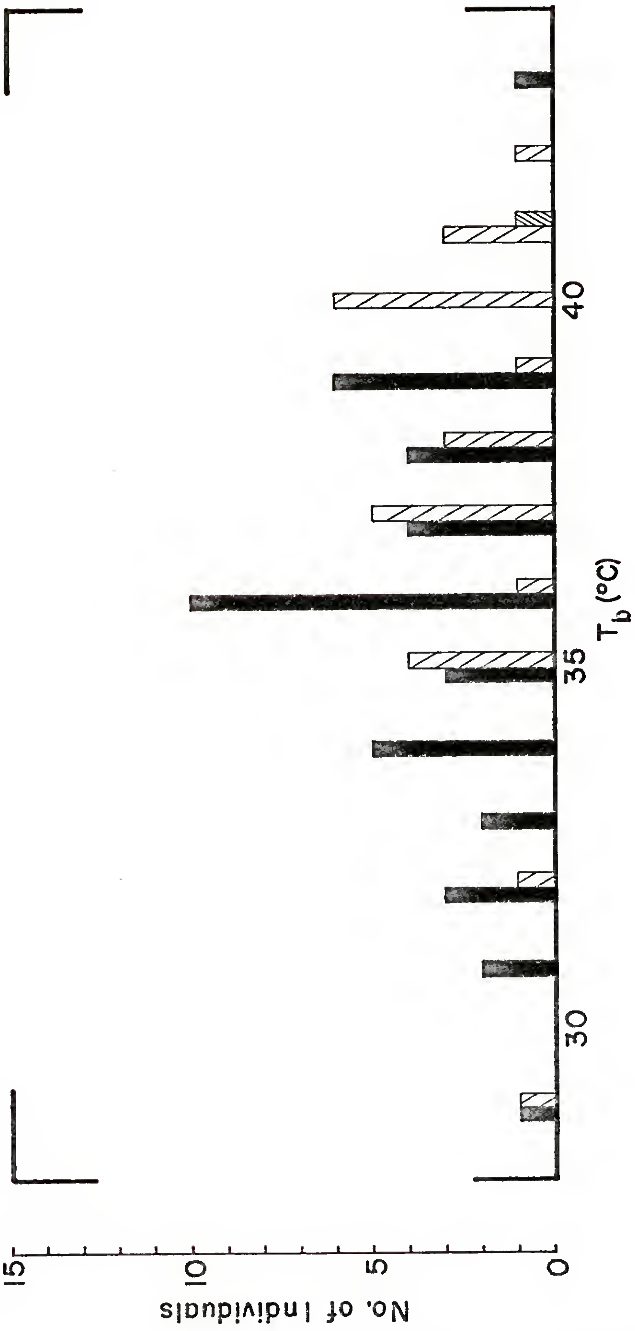

Perch Height (inches)
28
24
20
16
12
8
4
0
16
20
24
28
32
36
T_a (°C)

moderate T_b of 37.9°C. Three specimens were perched high at T_a below 25°C, but of these one was on a large, horizontal, light-colored log and another was on a broad leaf with its back to the sun. Thus, when ambient conditions are generally cool, there definitely appears to be a preference for broad surfaces, which may have a boundary layer of relatively warm air. The trend is especially evident because most observations were made in an area with extensive patches of bare ground. Other observations indicate that *E. simplicicollis* will perch on the surface of lawns or litter at higher air temperatures than shown here.

There is some relation between wing position and temperature, as seen in Figure 11. Again the wings tend to be depressed at low T_b. At high T_b they are generally flat, seldom elevated.

Is *E. simplicicollis* a more or less effective regulator than *Pachydiplax*? A comparison of the regressions of T_b on T_a (Table 4) suggests an answer, but the result is equivocal for two reasons. First, many *Pachydiplax*, unlike most *Erythemis*, were taken at breeding sites, where reproductive activity may reduce the time spent in thermoregulation. Second, somewhat different criteria were used in calculating the regressions for the two genera. This stems from the facts that less data were available for *Erythemis* and that no posture in that species was recognized as being a neutral response to temperature. Thus, it is difficult to define satisfactory behavioral criteria for animals that have less than optimal temperatures.

Figure 11. Frequency distribution of wing position as a function of T_b in *Erythemis simplicicollis*. Symbols as in Figure 5A.


No. of Individuals
0
5
10
15
30
35
40
T_b (°C)

The time of measurement was used to separate body temperatures that represent initial warming from nighttime levels from those that represent a regulated level. The thin irregular line on Figure 9 connects, in chronological order, points representing specimens collected from 0800 to 1030 on 12 August 1972. The early points indicate that T_b was rising much faster than T_a. At about the time indicated by the transition from open to closed circles (0900), T_b became much more constant and thereafter rose less rapidly than T_a, although all perched individuals were still in postures scored as increasing incident solar radiation until about 1000. Therefore, all measurements taken before 0900 were excluded from the regression of T_b on T_a. The change in the relation of T_b to T_a seen at about 0900 may be due to some subtle behavioral change that was not detected by direct observation, but as Heath (1964) has shown, this conclusion can be misleading and can be accepted only with some reservation. However, since certain postures in *Erythemis* are clearly correlated with temperature, and since the break in the T_b vs. T_a curve is fairly sharp, the supposition seems to be justified. Of course, the length of time the insects must spend basking will vary with latitude, season, cloud cover, and other factors, so no particular hour will be the proper cut-off point in all cases.

If the regression equations of T_b on T_a are accepted at face value, *E. simplicicollis* appears to thermoregulate a little better than *Pachydiplax*; it also has a body temperature about 1°C higher than the latter. The higher T_b is probably related to the tendency of *Erythemis* to perch on or near the ground. Females may control T_b

a bit more precisely than males (Table 4). Males are also usually smaller than females, and there is some indication in Table 4 that large specimens regulate better than small ones. Tethered individuals show no sign of regulation (Figure 12).

Erythemis plebeja is a tropical species, slightly smaller than *E. simplicicollis*, and these species are similar in their habit of perching on or near the ground and in the perching postures they assume. *Erythemis plebeja* differs strikingly from *E. simplicicollis* in two respects. First, females tend to perch in or near shaded areas much more than males. Second, the bodies of mature males are completely black. The males are also somewhat more slender than males of *E. simplicicollis*. All the data presented here pertain to males, mostly away from breeding sites.

Erythemis plebeja was studied at BCI, a lowland tropical location at which air temperature varied very little. This does not mean that the thermal conditions experienced by this dragonfly are constant. For example, the temperature registered by a shielded black bulb thermometer ranged from 30.9°C to 47°C, and that of an unshielded black bulb about one cm above the ground varied from 29.5°C to 53°C. However, given the scatter normally found in behavioral thermoregulators, a wide range of T_a is required to demonstrate thermoregulation, so it is not surprising that a plot of T_b vs. T_a (Figure 13) does not convincingly demonstrate temperature regulation.

Some evidence suggests that *E. plebeja* employs thermoregulatory behavior. In the laboratory clearing at BCI they are active from shortly after sunrise until late afternoon. During the early and late portions of this period, when sunlight at ground level is limited,

Figure 12. Relation of T_b to T_a in tethered *Erythemis simplicicollis*. Symbols as in Figure 7. For specimen in the sun $T_b = 0.99\ T_a + 6.61$, $r = 0.917$; for specimens in the shade $T_b = 0.98\ T_a + 2.69$, $r = 0.983$.

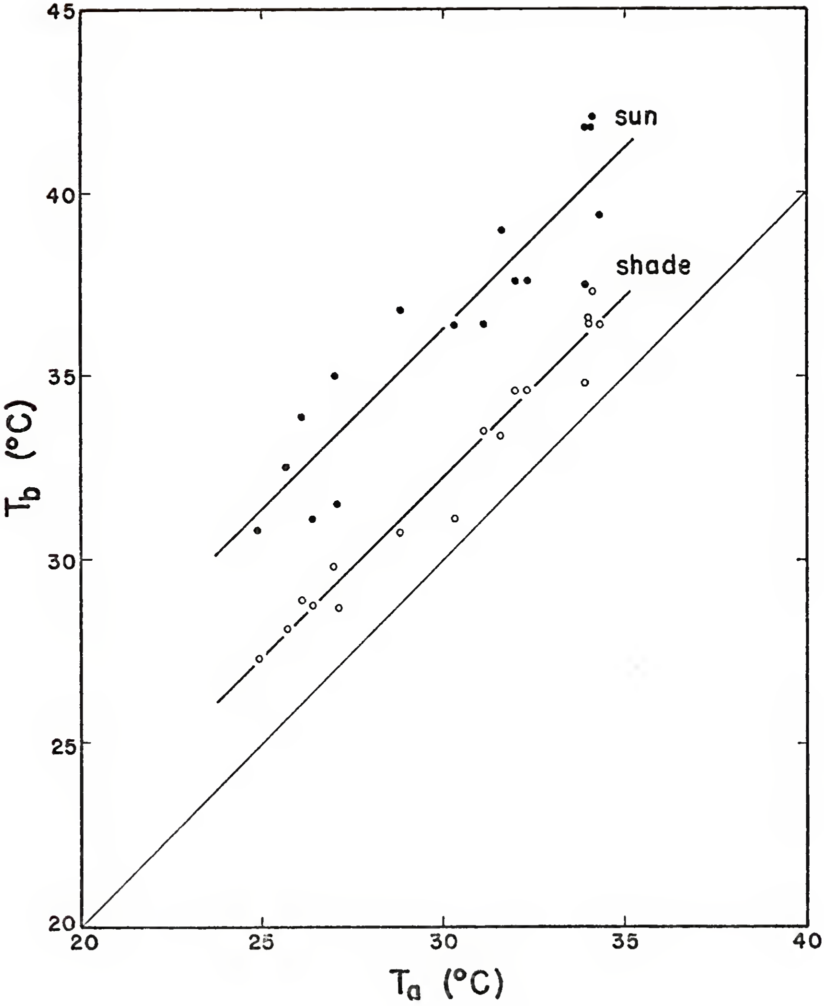
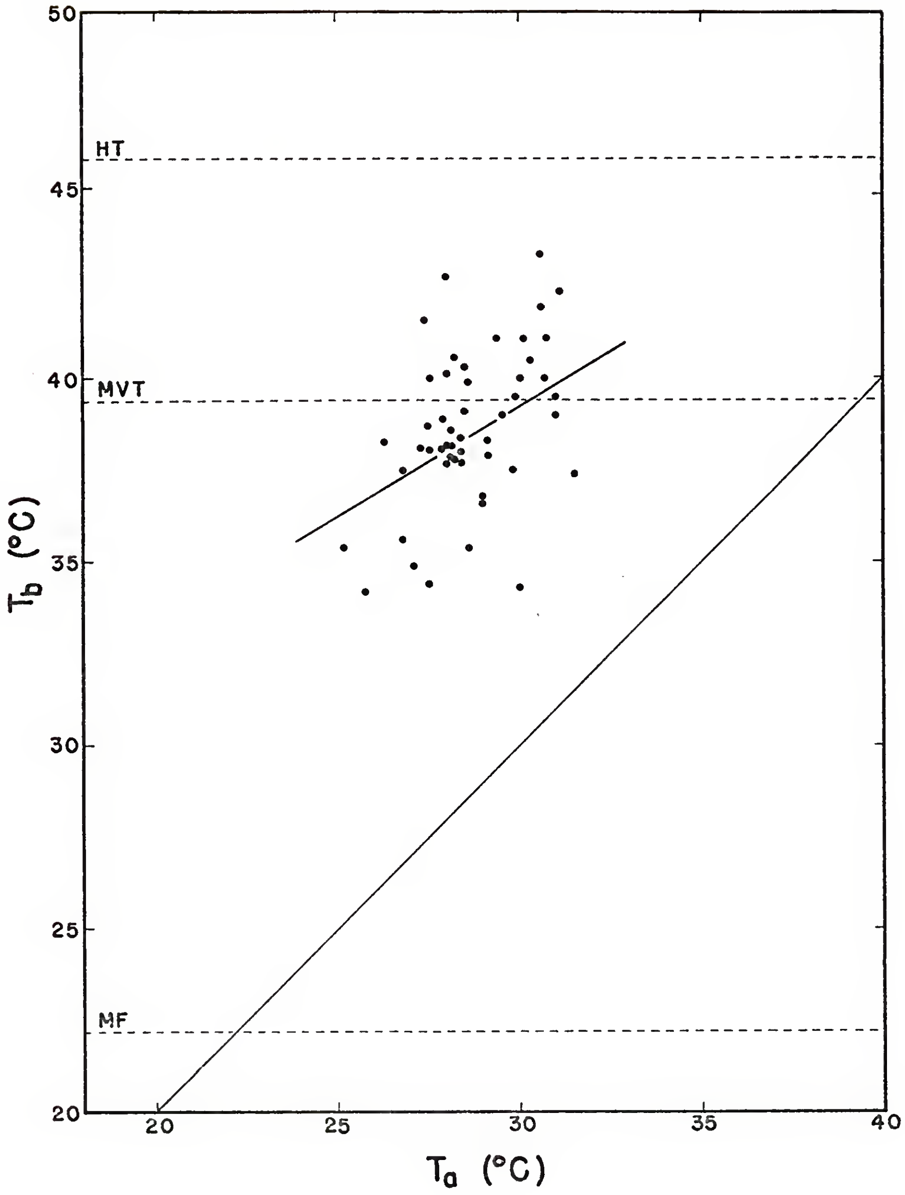

45
40
35
30
25
20
Tb (°C)
20
25
30
35
40
Ta (°C)
sun
shade
8

Figure 13. Relation of T_b to T_a in free-ranging *Erythemis plebeja*. Symbols as in Figure 8.


50
45
40
35
30
25
20
HT
MVT
MF
20
25
30
35
40
T_b (°C)
T_a (°C)

males appear to perch almost exclusively in the sunny patches. *Erythemis plebeja* also shows a tendency to perch either perpendicular to or with the dorsal surface exposed to the sun at low temperature (Figure 14). There did not appear to be any clear-cut heat avoidance posture, nor was there any evident relationship between perch height and temperature.

There is another line of evidence to suggest that thermoregulation may occur. Figure 15 shows the frequency distribution of body and air temperature for specimens tethered in the sun or free-ranging. The variance of T_a is similar for both groups (1.65 for tethered specimens, n = 33; 2.03 for free-ranging, n = 54), but the variance of T_b is much higher for tethered individuals (7.12) than for free-ranging ones (4.24). The value of the ratio of variance is the Fisher index, F. For T_b, F = 1.68, which indicates that the variances of these two populations are significantly different (p = 0.95). The mean T_b for free-ranging *E. plebeja* (38.6°C) is about 3°C higher than in tethered specimens (35.8°C) despite almost identical mean T_a. This observation may reflect the fact that free individuals perch near the ground while tethered ones were held three feet above the ground. The difference in height should tend to reduce the difference in variance if anything, because, as already discussed, T_a is generally more variable near ground level.

Examination of tethered specimens may also indicate the influence on T_b of the black color of *E. plebeja*. Table 5 shows that although determinations of T_b in tethered *E. simplicicollis* were made under conditions of greater radiant heat load, T_b of exposed specimens of

Figure 14A. Frequency distribution of posture as a function of T_b in *Erythemis plebeja*. Symbols are as follows: ▓ - perpendicular posture, ▧ - postures in which the specimen faced away from the sun with the adbomen depressed, exposing its dorsal surface, ▨ - all other postures.

Figure 14B. Posture as a function of T_a in *E. plebeja*; otherwise as in A.

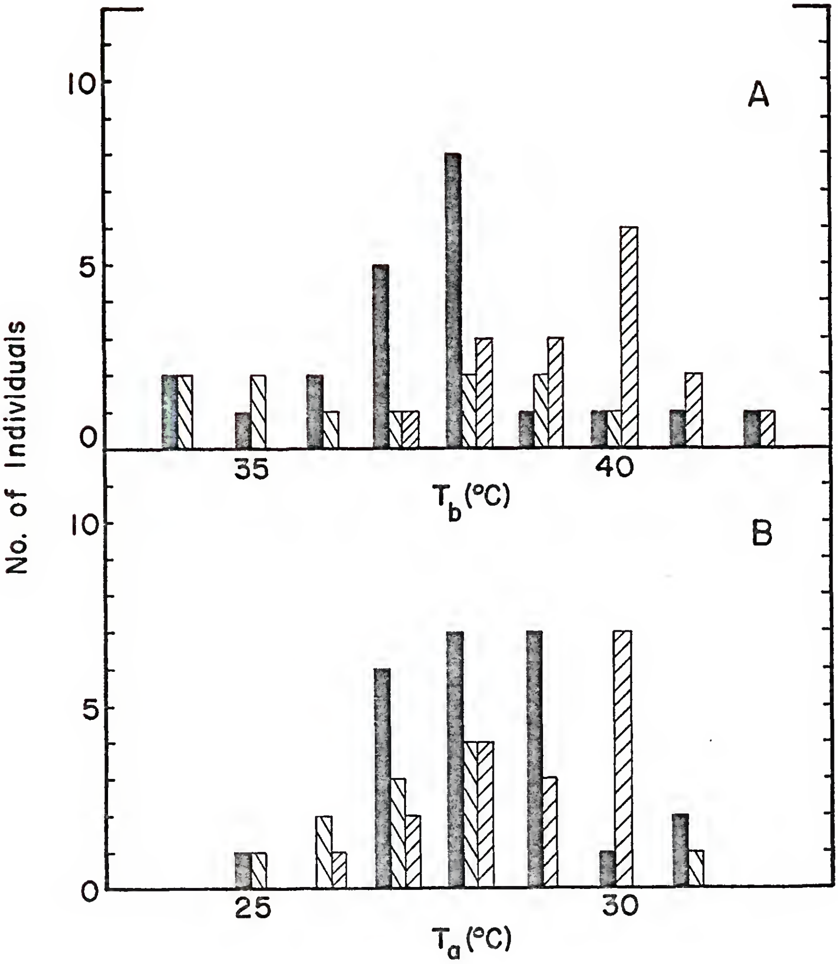

A
B
No. of Individuals
0
5
10
35
40
T_b (°C)
25
30
T_a (°C)

Figure 15A. Frequency distribution of T_b (■) and T_a (▨) in free-ranging *Erythemis plebeja*. Variance of T_a = 2.03, variance of T_b = 4.24, n = 54.

Figure 15B. As in A, tethered specimens of *E. plebeja*. Variance of T_a = 1.65, variance of T_b = 7.12, n = 33.

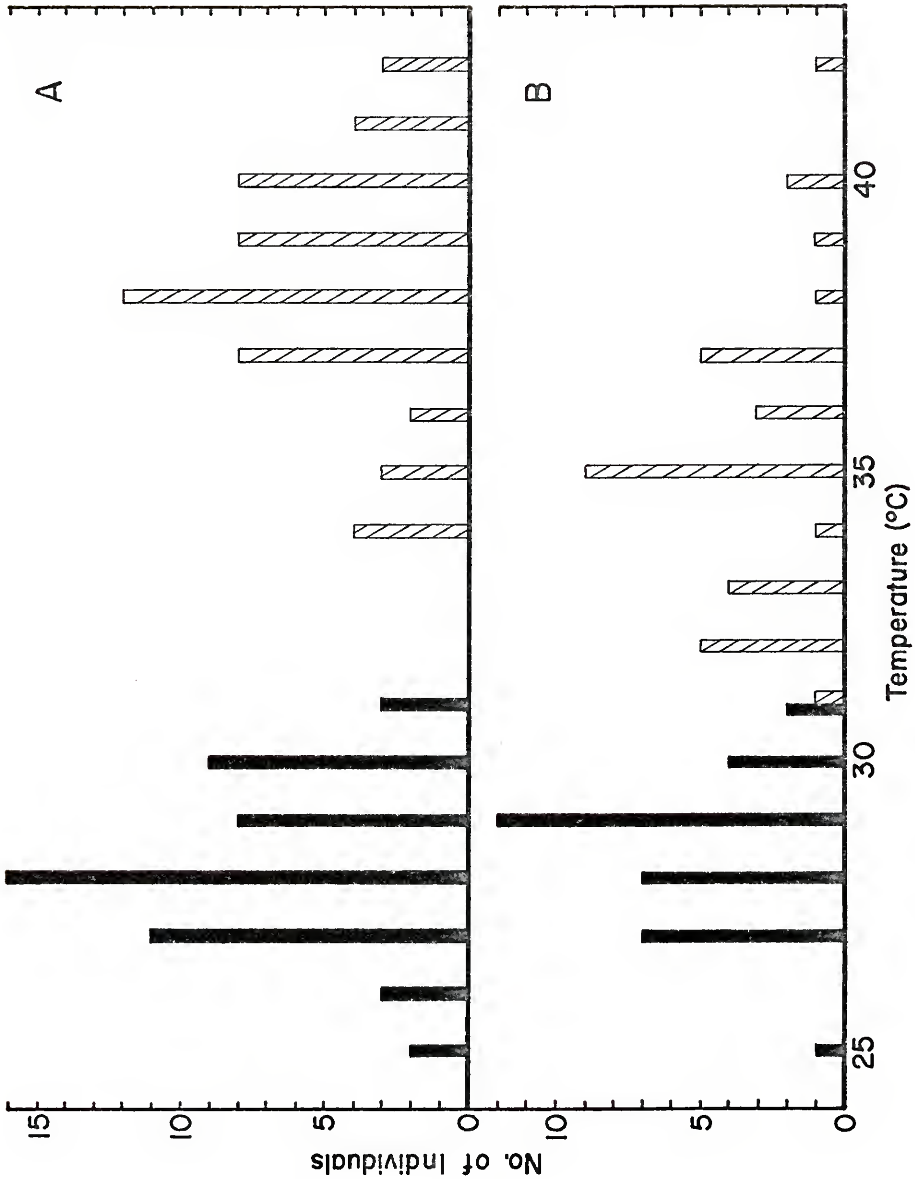

A
B
No. of Individuals
15
10
5
0
10
5
0
25
30
35
40
Temperature (°C)

Table 5. Relation of T_b to T_a in tethered specimens of *Erythemis; Erythemis simplicicollis* is green, *Erythemis plebeja* is black.

Species	Mean T_a $\pm$ S.D.	Mean T_{BB} $\pm$ S.D.	Mean $T_b - T_a$ $\pm$ S.D.	Max. $T_b - T_a$
Erythemis simplicicollis	30.2 ± 3.41	46.0 ± 5.08	6.32 ± 1.47[a]	8.0
Erythemis plebeja	28.9 ± 1.29	37.9 ± 4.12	6.84 ± 2.23[a]	12.3

[a] Probability that mean of *E. simplicicollis* is less than that of *E. plebeja* is about 0.85 (one-tailed Student's t test).

E. plebeja exceeded T_a to a greater extent. Some of the difference in mean black bulb temperature is due to cooling of the imperfectly shielded bulb by the almost constant trade wind at BCI. The dragonflies will be cooled by the wind also, of course, but not necessarily to the same extent. Nevertheless, it appears likely that the black color of *E. plebeja* results in a greater elevation of T_b above T_a than the mostly green *E. simplicicollis* can maintain under similar circumstances.

Maximum voluntarily tolerated temperature and the temperature at which heat torpor occurs are both slightly lower in *E. plebeja* than in *E. simplicicollis* (Table 13). Note, however, that *E. plebeja* is more likely in the field to exceed its maximum voluntary tolerance and to approach the effective lethal temperature than is *E. simplicicollis*. This suggests that the black color of *E. plebeja* is thermally disadvantageous and therefore probably evolved in response to some other selection pressure.

Libellula spp.

The following account refers to the two sibling species (Paulson, 1966), *Libellula auripennis* and *L. needhami*, which are treated together. They are usually indistinguishable in the field, although they can be readily separated in the hand. Through an oversight they were not distinguished in collections made in 1972. However, all data are from the same site, an open field where no breeding activity took place. Since all collections made in 1973 comprised at least 75% and usually 80-100% *L. needhami* there is little doubt that 80% or more of the data refer to the latter species. In any case, Paulson (1966) was not able to discover any difference in habitat or behavior between adults of the two species, nor have I, so conclusions about one are probably equally applicable to the other. The species are about the same size (body weight - 0.495 g).

Figure 16 is a plot of T_b vs. T_a for *Libellula*. Again, tenerals and individuals taken when sunlight was not available are excluded. It is immediately evident that T_b is substantially less variable than T_a. Figure 17 shows that if these dragonflies are tethered either in sun or shade, temperature regulation is abolished.

Libellula accomplishes regulation with behavior patterns similar to those of *Erythemis*. Figures 18A and B are the frequency distributions of various body postures. These postures are similar to those already described for *Erythemis*. Postures maximizing solar exposure may be maintained over a wide range of T_b, but they are mostly restricted to low T_a. Heat avoidance postures are strictly associated with high T_b.

These dragonflies were also scored in a different way (Figure 18C). Individuals recorded as perching on the "sun side" were on the sides of erect stems facing almost directly away from the sun, with their abdomens and thoraxes depressed, thus maximally exposing their thoracic dorsum. Those scored on the "shade side" were in the corresponding mirror image position and were partially shaded by their perch. This division of postures makes possible a sharper distinction between individuals actively seeking or avoiding radiant heat input.

Libellula evidently never perches on the ground, and there seems to be no correlation between temperature and perch height. There is also no apparent relation between wing position and temperature: of seventy non-teneral individuals in which wing position was scored, fifty-seven held their wings flat, and when the wings were depressed or elevated

Figure 16. Relation of T_b to T_a in free-ranging *Libellula*. Symbols as in Figure 8.

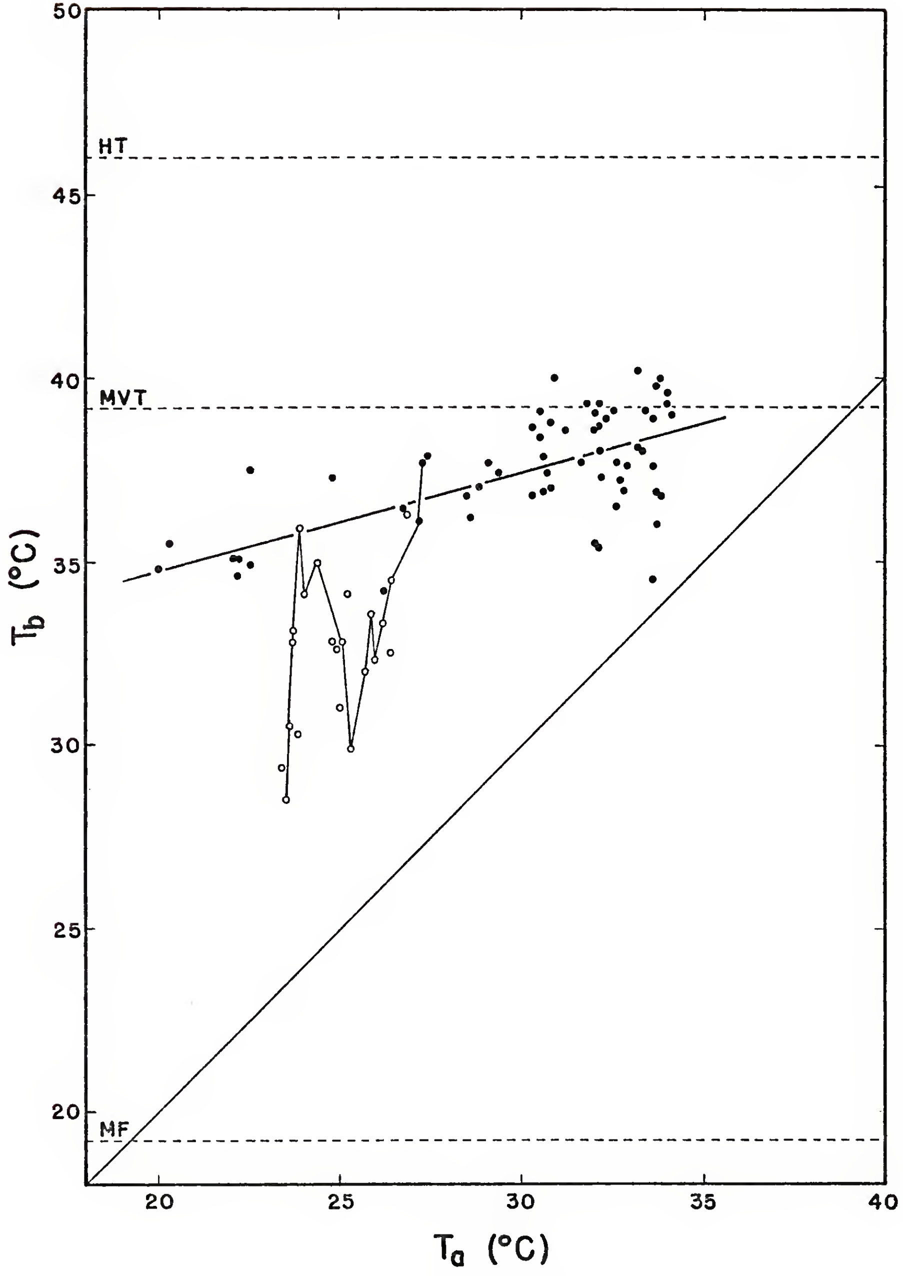

50
45
40
35
30
25
20
HT
MVT
MF
T_b (°C)
20
25
30
35
40
T_a (°C)

Figure 17. Relation of T_b to T_a in tethered *Libellula*. Symbols as in Figure 8. For specimens tethered in the sun $T_b = 0.92\ T_a + 11.12$, $r = 0.888$; for specimens in the shade $T_b = 1.00\ T_a + 2.74$, $r = 0.975$.

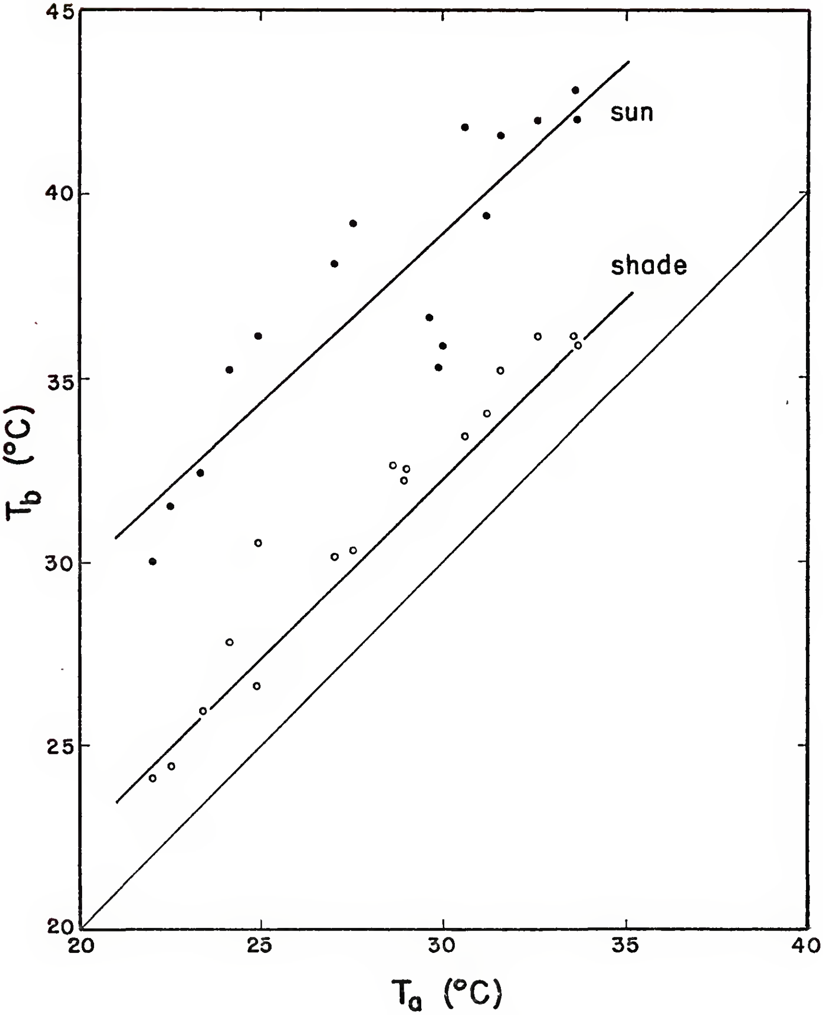
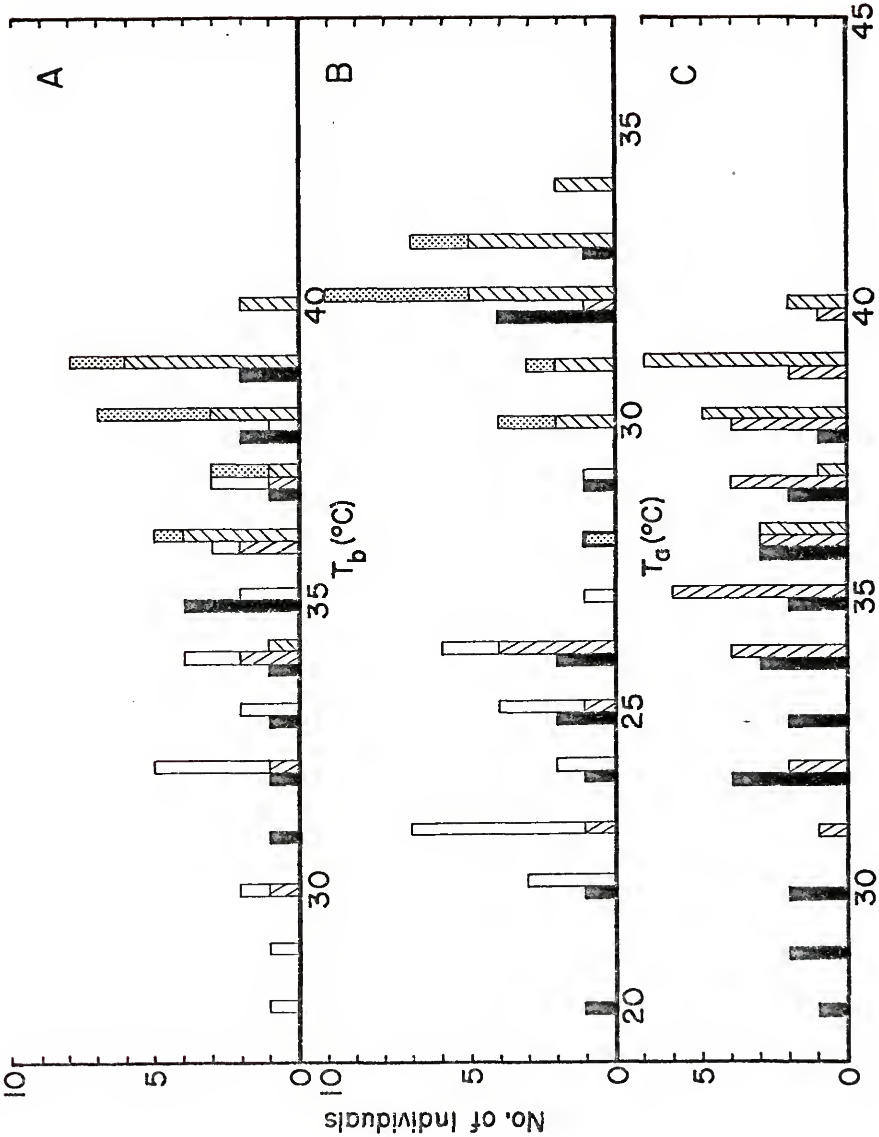

sun
shade
45
40
35
30
25
20
20
25
30
35
40
T_b (°C)
T_a (°C)

Figure 18A. Frequency distribution of posture as a function of T_b in *Libellula*. Symbols as in Figure 9.

Figure 18B. Posture as a function of T_a in *Libellula*; otherwise as in A.

Figure 18C. Overall position as a function of T_b in *Libellula* (see text). Symbols are as follows: ■ - specimens on sun side of stem, ▨ - those on shade side of stem, ▧ - those not scored as being definitely on one side or the other.


A
B
C
No. of individuals
0
5
10
T_b (°C)
T_a (°C)
20
25
30
35
40
45

the departure from the flat position was usually small.

The regression of T_b on T_a was calculated in the same way as for *Erythemis*, except that the cut-off time for excluding data from the calculation was 0930. The slightly later time may be due to the fact that *Libellula* does not usually perch on or very near the ground and thus is restricted to less rapidly warming air strata.

The data from 11 July 1972 illustrate that the heterogeneity of the habitat is another complicating factor in measuring thermoregulatory behavior. Note that on this date T_b determinations showed an initial sharp rise, followed by an almost equally precipitous fall, followed by another rapid increase. The fall in T_b records occurred as I worked my way across the field. This field is surrounded by trees, so in early morning the west side receives sunlight before the east side. Dragonflies on the west side could therefore attain elevated T_b before those on the east side. Clearly the individuals in the shaded areas could elevate their body temperatures by flying to the sunny region, since they can fly if disturbed and the field is only 45 to 50 m across, but they apparently do not do so. *Erythemis simplicicollis* in the same field does tend to be somewhat more concentrated in the sunny areas, although many individuals remain in the shade. *Libellula* apparently remain on their nocturnal perches on grass stems, oriented randomly, until sunlight reaches them. From about mid-morning on, only tenerals are found in the shade, indicating that adults avoid shade after they become fully active. On the very hottest days there seems to be some tendency for adults to concentrate near the edges of shaded areas.

Table 4 shows that at least from mid-morning to late afternoon, *Libellula* thermoregulates much better than either *Pachydiplax* or *Erythemis*, both in terms of the independence of T_b and T_a and of the the variation in T_b at a given T_a. Males appear to regulate somewhat better than females, but this may be misleading. Males are much more wary than females, especially at high temperatures, so fewer of the former were collected.

Trameinae

Five species of this subfamily, belonging to the genera *Miathyria*, *Tauriphila*, and *Tramea*, were studied. They were generally collected in feeding swarms in which there was no reproductive activity. These dragonflies are quite uniform structurally and behaviorally and are very different from the other libellulids considered so far. The most important difference in terms of their thermal relations is that they are fliers, although they will perch occasionally. They also can elevate their body temperature by wing-whirring, an ability which the previously discussed species lack. All the trameines have their hind wings expanded basally (*Tauriphila* less so than the others), and all are primarily diurnal, although *Tramea carolina* may fly at dusk. Figures 19-22 show the relationships between T_b and T_a in these dragonflies. In these four figures all data on non-teneral specimens are included, whether or not sunlight was available. Specimens taken during sunless periods, as well as those not in flight, are indicated. *Tramea cophysa* and *T. walkeri* (= *binotata*?) are treated together because females of these species could not always be distinguished.

Figure 19. Relation of T_b to T_a in free-ranging *Tramea carolina*. Symbols as in Figure 8 except as follows: • - specimens in flight in sun, + - specimen in flight with sun not available, ∘ - specimen perched.

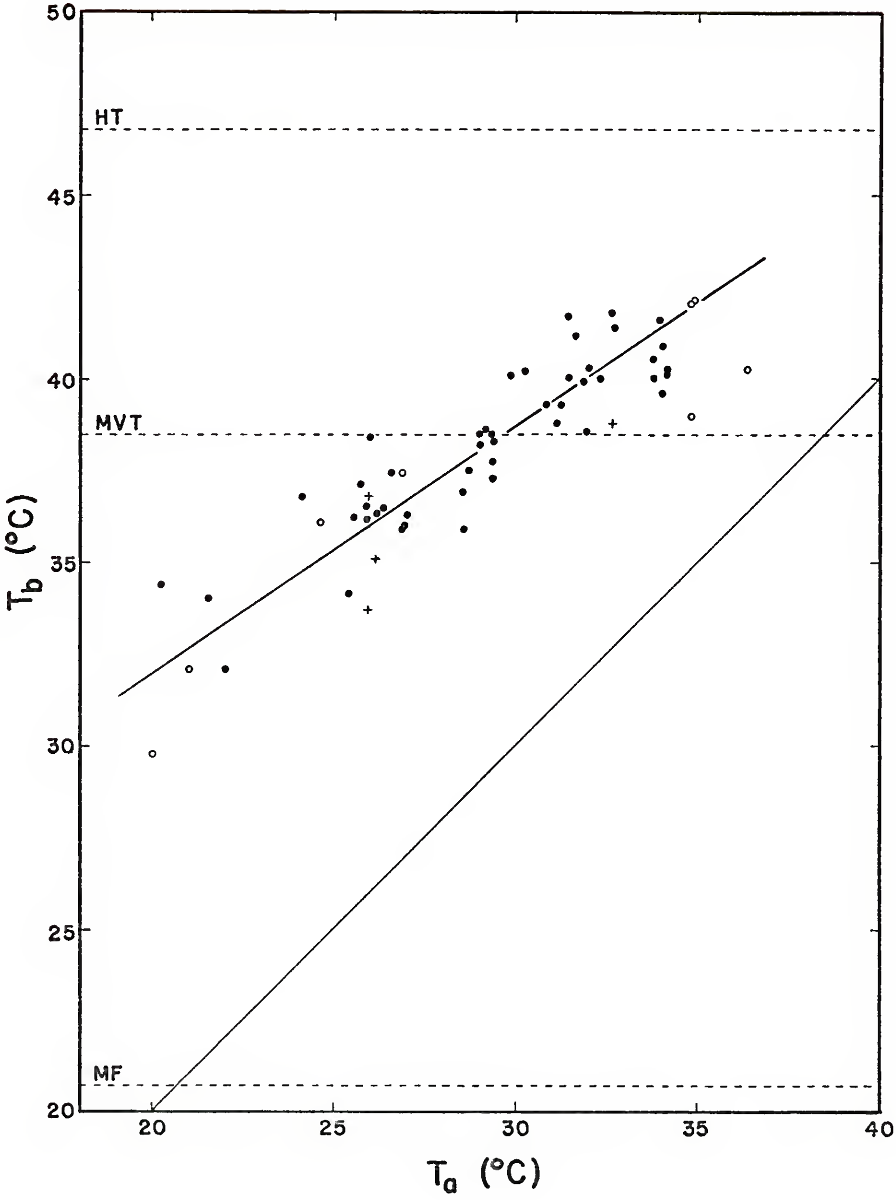

50
45
40
35
30
25
20
HT
MVT
MF
T_b (°C)
20
25
30
35
40
T_a (°C)

Figure 20. Relation of T_b to T_a in free-ranging *Tramea cophysa* and *Tramea walkeri*. Symbols as in Figure 19; ● - specimens perched with sun unavailable.

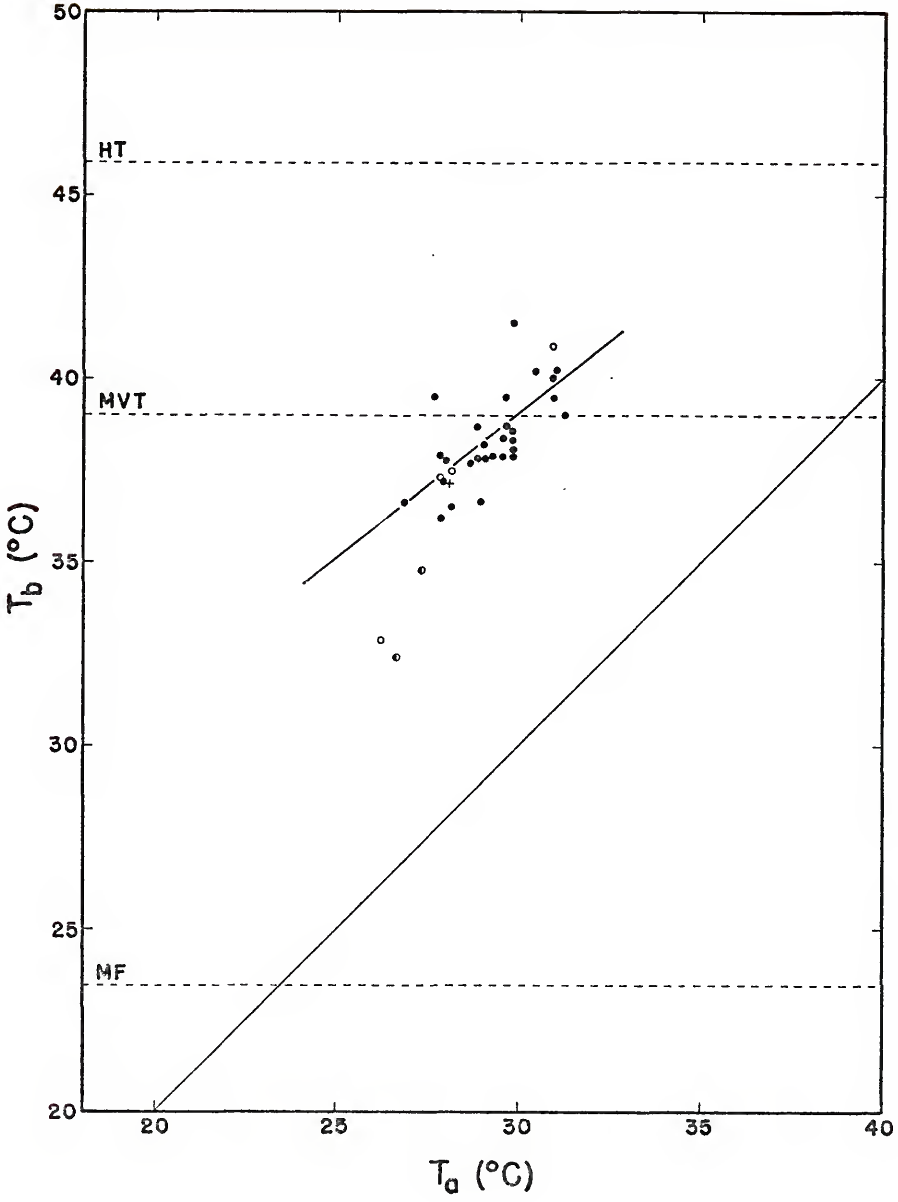

HT
MVT
MF
50
45
40
35
30
25
20
20
25
30
35
40
T_b (°C)
T_a (°C)

Figure 21. Relation of T_b to T_a in free-ranging *Tauriphila argo*. Symbols as in Figure 19.

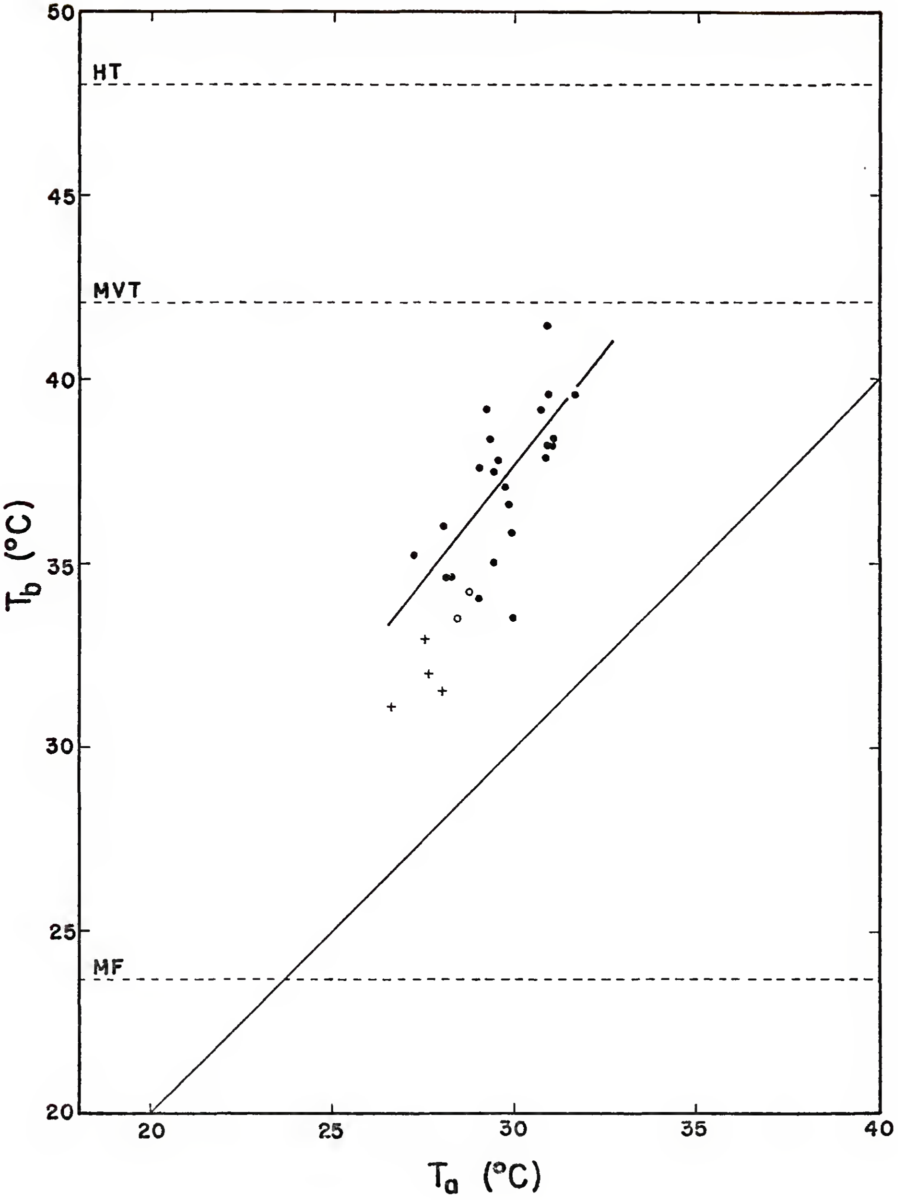
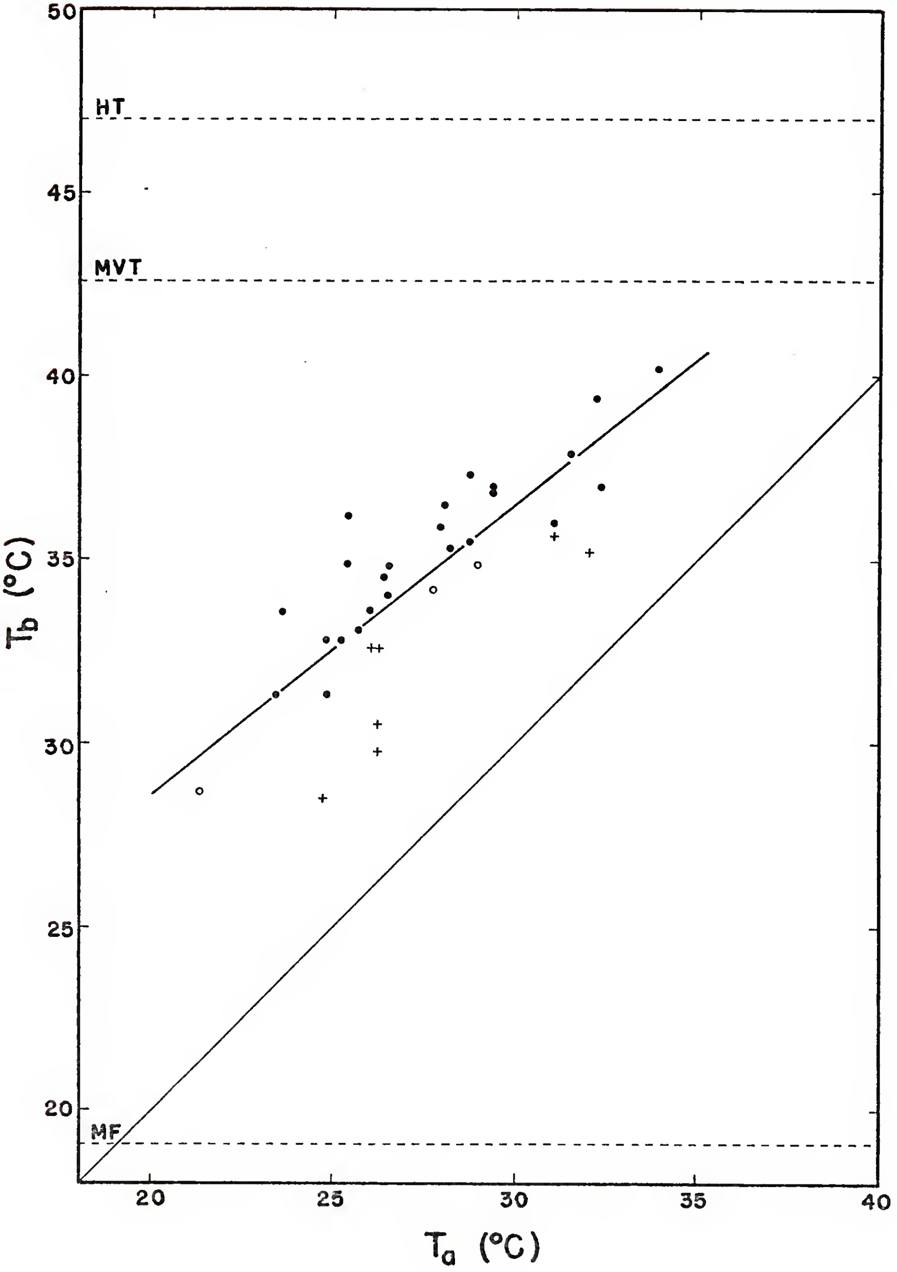

50
45
40
35
30
25
20
HT
MVT
MF
20
25
30
35
40
Tb (°C)
Ta (°C)

Figure 22. Relation of T_b to T_a in free-ranging *Miathyria marcella*. Symbols as in Figure 19.


HT
MVT
MF
50
45
40
35
30
25
20
T_b (°C)
20
25
30
35
40
T_a (°C)

Judging from measurements of males there is no difference in eccritic temperature, despite the fact that males of *walkeri* are black. Both species flew together at the BCI laboratory clearing.

These figures and Table 4, indicate that none of the Trameinae thermoregulate as well as the perchers discussed above. Only in *Tramea carolina* is there a clear indication of regulation. The relative lack of control of T_b is not primarily due to the inclusion in the graphs of individuals that did not have access to sun. In *Miathyria* T_b is somewhat higher when sun is available, but regulation is not much improved. If data from sunless periods are left out, the regression equation is $T_b = 0.77\ T_a + 14.0$ (*c.f.* Table 4). In the Panamanian *Tramea*, perched specimens taken during cloudy periods or very early in the morning had much lower body temperatures than other individuals and so are excluded from the regression of T_b on T_a. It is interesting that there sometimes seems to be a tendency for *Tramea* to stop flying when it is cloudy, even though this action evidently results in a reduced T_b.

There is little evidence that these species actively bask or otherwise alter their behavior to control radiant heating. Perched *Tramea* may sometimes adjust the posture in response to sunlight. Corbet and Eda (1969) recorded *Tramea lacerata* in Canada apparently basking by exposing their dorsal surface to the sun. A flying dragonfly might possibly orient its flight path so as to optimize the amount of incident radiation. However, my field experience firmly suggests that the flight pattern in all these species is random in relation to the sun.

Nevertheless, in *Tramea carolina* the slope of T_b on T_a is substantially less than 1.0 (Table 4). Much of the difference between T_b and T_a in these dragonflies must be due to the heat produced by the thoracic muscles during flight, since a large differential is maintained in the absence of sunlight (Figure 19). Such thermoregualtion as does occur must be primarily the result of control of either the production or the loss of metabolic heat. Thus, *Tramea carolina* may fairly be considered a periodic endotherm.

Heinrich and Bartholomew (1971), Heinrich and Casey (1973), and Bartholomew and Casey (1973) have made a strong argument that in moths only heat loss, and not heat production, is controlled, despite the earlier conclusions of Heath and Adams (1967) and McCrea and Heath (1971). This need not be the case in all insects, however. Hankin (1921) noted that various Trameinae mostly use gliding rather than powered flight during hot, sunny days, but seem to flap their wings continuously at twilight and in early morning. Corbet (1963) and Miller (1962) both noted similar behavior, and Corbet suggested that the expanded anal margin of the hind wing of many species is an adaptation for gliding.

My own observations confirm that at high T_a in sunny weather *Tramea carolina* spends most of its time gliding, with only occasional flaps. When flying at dusk or during cloudy periods its flight is much more erratic, with little gliding, if any. This distinctive flight pattern also occurs in *Tramea walkeri* in late afternoon. However, flight on cool but sunny days does involve some gliding, suggesting that solar heating can substitute for some of the metabolic heat generated by flapping.

Tramea carolina also apparently adjusts heat loss, as shown by the progressive increase in the cooling constant as T_a is raised from 15°C to 30°C (Table 10 and Figures 30-33). This increase is apparently due to increased circulation of blood from the thorax to the poorly insulated abdomen and thence the loss of heat by convection to the air (see p. 138). Heat loss is further augmented because at high ambient temperature *Tramea carolina* frequently fly with their abdomens strongly depressed, sometimes at angles of 45° or more below the horizontal. This reduces exposure of the abdomen to radiant heating and may increase convective cooling by reducing the effect of the thorax as a wind shield on the abdomen. This behavior seems never to occur on cool days or during the erratic, powered flight at dusk.

Hankin (1921) noted the same phenomenon in flying trameines in India. He believed that its function was to brake airspeed. It may sometimes have this function, as flying birds lower their legs and tail when slowing for a landing (Pennycuick, 1971). However, Hankin's own data lend strong support to the association of this behavior with a high heat load, since he noted that it occurs only near midday during the hottest months of the year and is abandoned if clouds obscure the sun.

All four specimens of *T. carolina* taken at ambient temperatures greater than 34.5°C were perched. These were all taken in early afternoon on a day when ambient temperature sometimes exceeded 37°C. One of them (T_b = 39.0°C) was hanging vertically in the shade, suggesting that it had been forced to suspend activity altogether. The others were perched at the tops of stems facing into a rather stiff breeze, all with their abdomens lowered sharply. These observations indicate that at T_a of 35°C and above this insect can remain active (in the sense that they remain alert and fly and feed at brief intervals) by becoming a percher. However, the windiness of that day presented rather special circumstances in that the dragonflies were able to reduce metabolic heat production while still being cooled by forced convection. On a still day at this temperature they might be forced either to continue flying, probably resulting in higher values of T_b than seen here, or seek shade and become temporarily quiescent.

Miathyria marcella is a very poor thermoregulator (Table 4). Although $\Delta T_b/\Delta T_a$ is significantly less than 1.0 ($0.95 < p < 0.975$), its biological significance is uncertain. If these dragonflies actually are actively thermoregulating, the mechanisms are probably similar to those of *Tramea*. *Miathyria* glides a good deal at high ambient temperatures and flies more erratically, with less gliding, early in the morning and late in the afternoon. The data in Table 8 do not indicate an increase in cooling constant with increasing temperature, but there may be a slight rise nonetheless (see p. 138).

A definite decrease in average T_b develops when sunlight is unavailable. This feature probably indicates that the ability of this species to increase heat production by abandoning gliding flight is less well developed than in *Tramea*, which is in accord with the impression that *Miathyria* is a weaker flier.

As already noted (p. 61), the data on the Panamanian species are not entirely comparable to those from Florida. The small ambient temperature range is bound to obscure evidence of body temperature regulation. However, because of the increased influence of forced convection in fliers, air temperature should give a much better picture of the thermal environments of the trameines than of *Erythemis plebeja*. *Tramea* (excluding the three perched specimens with low T_b, Figure 20) and *Tauriphila argo* (excluding data from cloudy periods, Figure 21) have higher correlation coefficients, 0.707 and 0.684 respectively, than *E. plegeja* (0.405). Since T_b clearly depends on T_a and the variation of T_b is not less than that of T_a, the argument against thermoregulation is stronger here than in the case of *Erythemis plebeja*. A comparison of the data on the tropical species of *Tramea* in flight with those of *Tauriphila* in flight shows that T_b is more variable in the latter species. This observation implies that, if regulation occurs at all, it is better developed in *Tramea*. *Tauriphila* is smaller than *Tramea* (Table 4).

The overall picture of the Trameinae is that they do not thermoregulate well because they cannot control radiant heat load, and they experience rather rapid convective heat loss, which tends to bring body temperature into equilibrium with air temperature. Large species like *Tramea* probably achieve some control of T_b by varying metabolic heat production and loss. Small species lose heat by convection even more rapidly than large ones, and their smaller metabolic heat production gives them less scope for adjustment. Consequently they exhibit still poorer regulation.

Anax junius

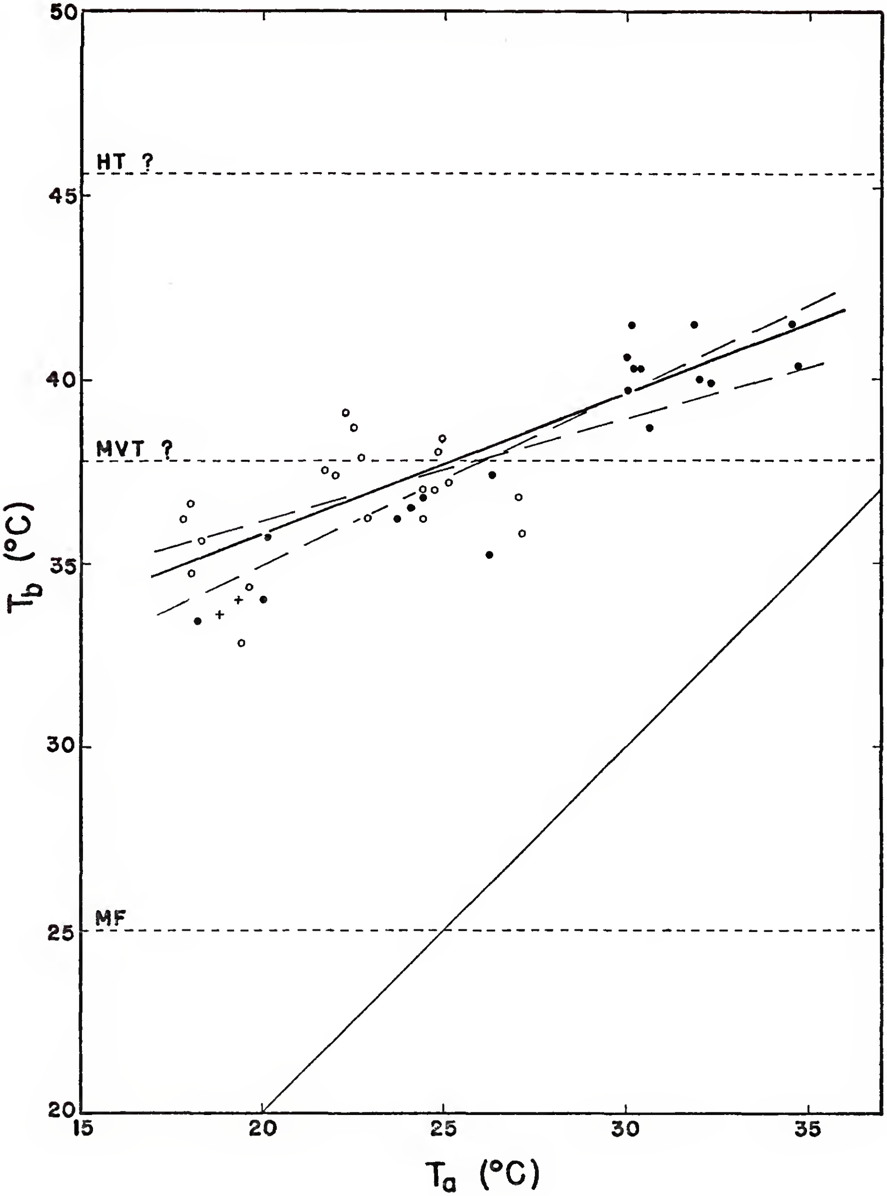
Like other Aeshnidae, this species is a flier, and a stronger, larger and more persistent one than the trameines. *Anax* generally remain on the wing continuously except when they cease actively for long periods, during which they hang vertically in sheltered places. However, unlike many other aeshnids, *Anax* will sometimes make short flights low in grass and hang intermittently on the stems (Corbet and Eda, 1969; unpublished personal observations). They may bask at this time.

Individuals are active during the hottest days and also occur commonly in crepuscular feeding swarms, sometimes flying until almost full dark. They may fly before sunrise, also. Since they are active near Gainesville from mid-March until November (apparently with a hiatus from mid-May until mid-July), they evidently face a very broad range of temperature.

Because it is a flier, *Anax* encounters the same problems as *Tramea carolina* in using solar radiation as a controllable heat source. It apparently does not modify its behavior in response to radiant heat load. Furthermore, this heat source is obviously not available during dawn and dusk flights. Yet *Anax* does thermoregulate, and it does so substantially better than *Tramea* (Table 4; Figure 23). *Anax* apparently has an even greater capacity for regulation than indicated in Figure 23, since I have seen individuals flying after sunset at an ambient temperature of 12°C. *Anax* will also warm-up at cool ambient temperatures by wing-whirring. This evidence leaves little doubt that *Anax* is an endotherm.

Females may regulate better than males (Table 4; see also p. 170). Unfortunately, all the females were collected during feeding flights at dusk with the exception of two hanging on grass stems and one

Figure 23. Relation of T_b to T_a in free-ranging *Anax junius*. Symbols as in Figure 3 except as follows: • - males in flight, ∘ - females in flight, + - perched females, dashed lines indicate regression of T_b on T_a in males and females separately.

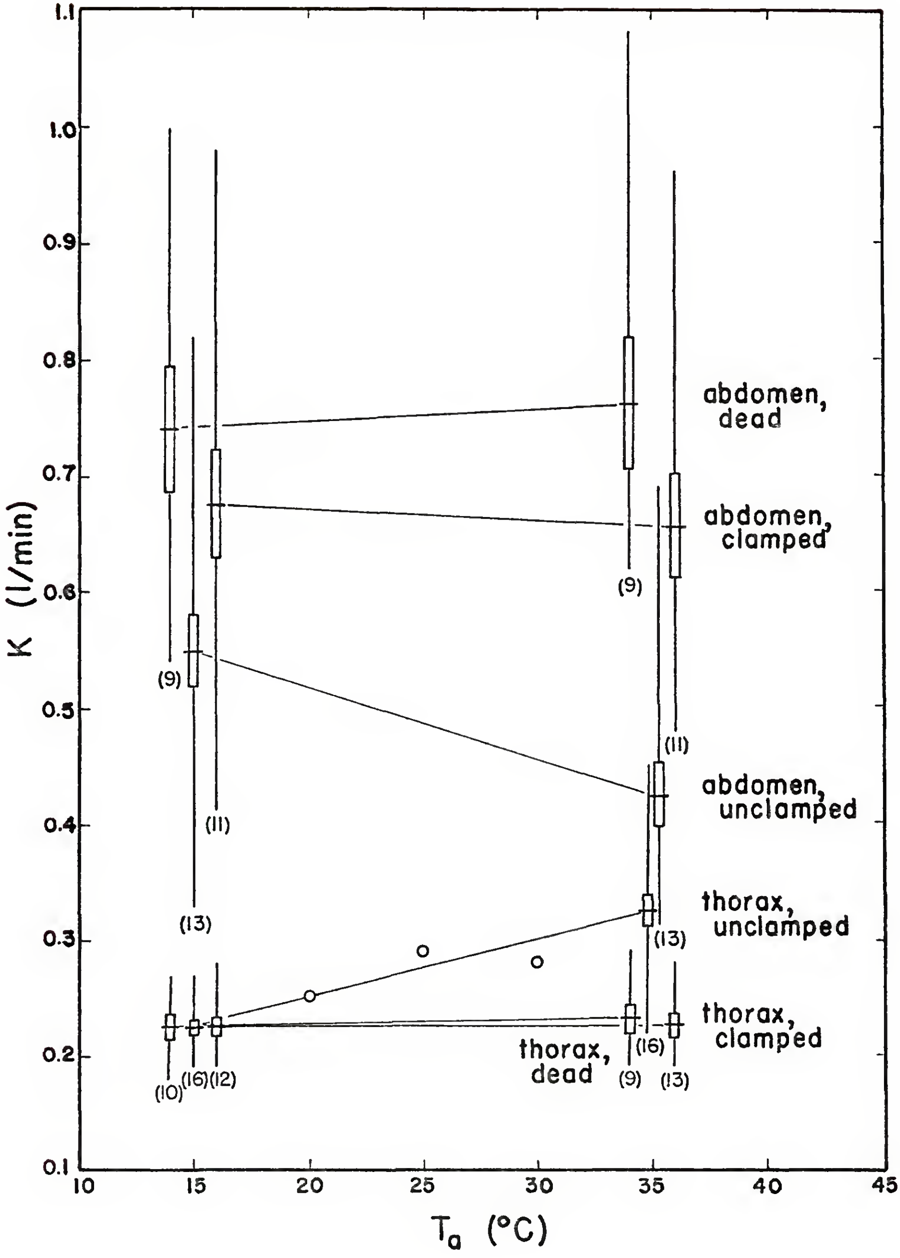

50
45
40
35
30
25
20
15
20
25
30
35
HT ?
MVT ?
MF
T_b (°C)
T_a (°C)

teneral individual. Thus it is not certain that the T_b of diurnally active females is less variable than that of males.

As with *Tramea*, the evidence that *Anax* controls heat production is indirect. Metabolic scope is certainly high since this species can maintain T_b at least 19°C above T_a in the field after sundown. *Anax* appears to glide for a high proportion of its flying time during midday and to use powered flight during crepuscular activity. Hankin (1921) refers to similar behavior in the closely related *Hemianax*.

Experiments in which circulation of haemolymph into the abdomen was restricted by means of a metal clamp clearly show that *Anax* controls heat loss by modifying abdominal circulation. Figure 24 summarizes the results, which comprise data from a few tenerals as well as mature individuals. Normal living individuals had a mean thoracic cooling constant at 15°C essentially the same as dead specimens. The abdominal cooling constant was substantially lower than in dead specimens, indicating that perhaps some circulation between the tagmata did take place. At 35°C the thoracic cooling constant had increased by almost 50% while the abdominal cooling constant had decreased sharply (the probability that the values at 15°C and 35°C are different is > 0.995 for both thorax and abdomen). This is precisely the response expected if large quantities of warm blood flowed into the abdomen, slowing the cooling of the latter but speeding cooling of the thorax. When the same individuals were tested with the base of the abdomen clamped off, the thoracic cooling constant remained about the same as in dead specimens regardless of T_a, again the result predicted by the hypothesis. The abdominal cooling constant is also essentially constant

Figure 24. Cooling constant of the thorax and abdomen as a function of T_a in live and dead *Anax junius*, with or without the abdomen clamped at the base. Horizontal lines indicate means, vertical lines ranges and vertical bars the extent of one standard error on either side of the mean. Open circles show means of thoracic conductance at intermediate temperature, from other experiments. Numbers in parenthesis show the number of individuals for each treatment.


K (l/min)
Ta (°C)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
10
15
20
25
30
35
40
45
abdomen, dead
abdomen, clamped
abdomen, unclamped
thorax, unclamped
thorax, clamped
thorax, dead
(9)
(13)
(11)
(9)
(11)
(13)
(10)
(16)
(12)
(16)
(9)
(13)

in clamped individuals, and it is higher than in unclamped specimens. It is slightly lower than in dead specimens, indicating that some haemolymph may have leaked past the clamp.

Theoretical difficulties exist in calculating a cooling constant by Newton's law from these cooling curves, mainly because the rate at which haemolymph circulates into the abdomen probably depends on thoracic temperature only and not on $T_b - T_a$ (Heinrich, 1970b). However, plots of $\Delta T_b/\Delta t$ on $T_b - T_a$ generally give straight lines, conforming to Newton's law. Often a rapid drop in the abdominal temperature occurred during the first minute of cooling, perhaps indicating a time lag before blood began to be shunted to the abdomen.

Another set of experiments supports the conclusion that abdominal circulation is important in heat transfer. The thorax was heated independently of the abdomen with a microscope lamp, and changes in thoracic and abdominal temperature were followed simultaneously. Figure 25 shows records from three experiments. These results are fairly typical except that sometimes at high T_a thoracic temperature would stabilize briefly, then rapidly rise to very high, often lethal, levels, as if some individuals gave up regulation. It is apparent that the increase of thoracic temperature is less at high T_a, while the reverse is true of abdominal temperature. Note also that in Figure 25A and B there is a very sharp slowing in the rise of thoracic temperature, with obvious departure of the curve from exponential form, and in Figure 25B there seems to be a simultaneous sharp increase in abdominal temperature. These data suggest that circulation is under voluntary control and does not simply increase

Figure 25A. Thoracic and abdominal temperature recorded in male *Anax junius* during local heating of the thorax at ambient temperatures of 15°C, 20°C, and 25°C, and in the same specimen at 25°C four hours after decapitation. Beginning of heating indicated by short vertical line. Arrows mark points at which base of abdomen was clamped off, then released. Note that at T_a = 25°C, thoracic temperature became constant after 15 minutes and remained so until the abdomen was clamped.

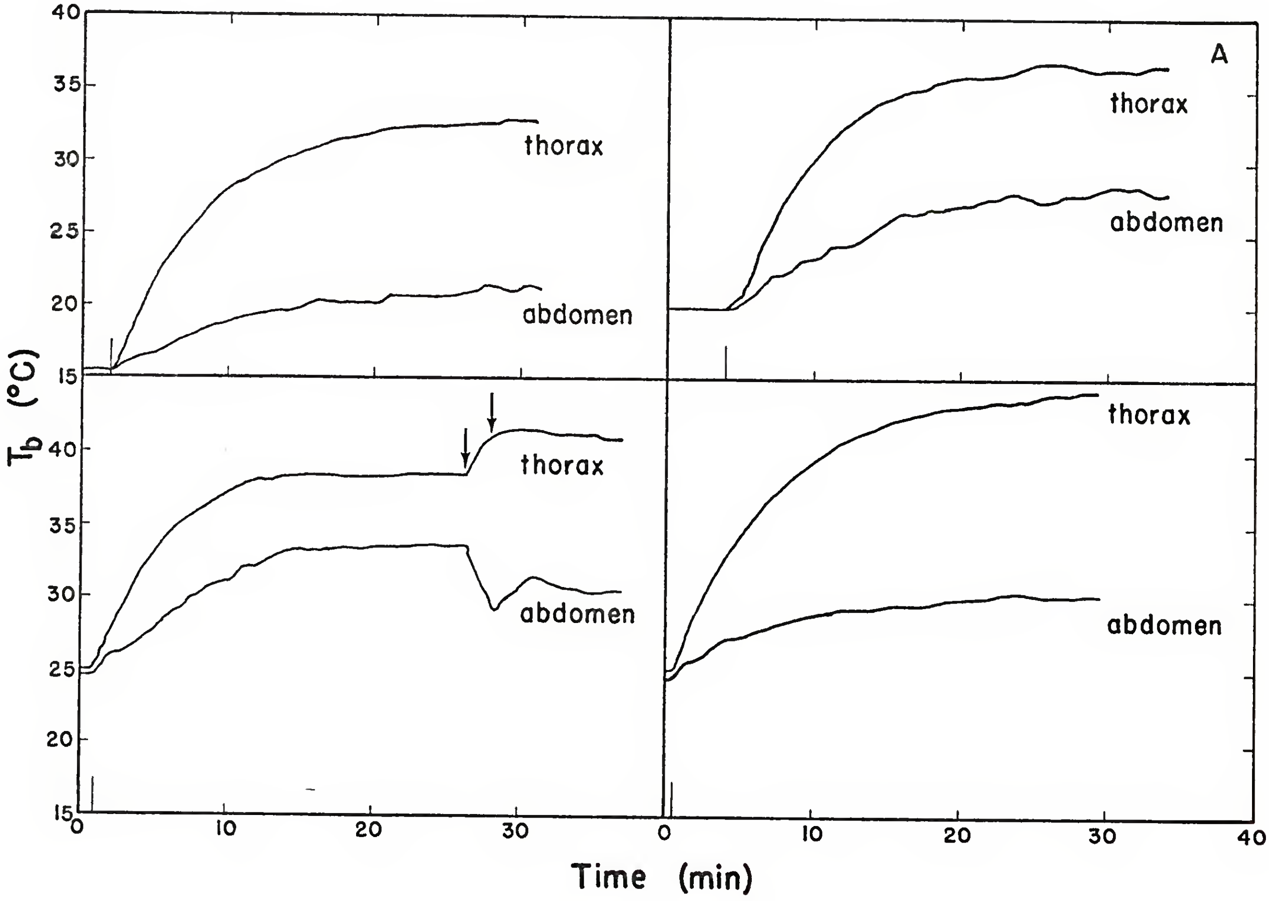
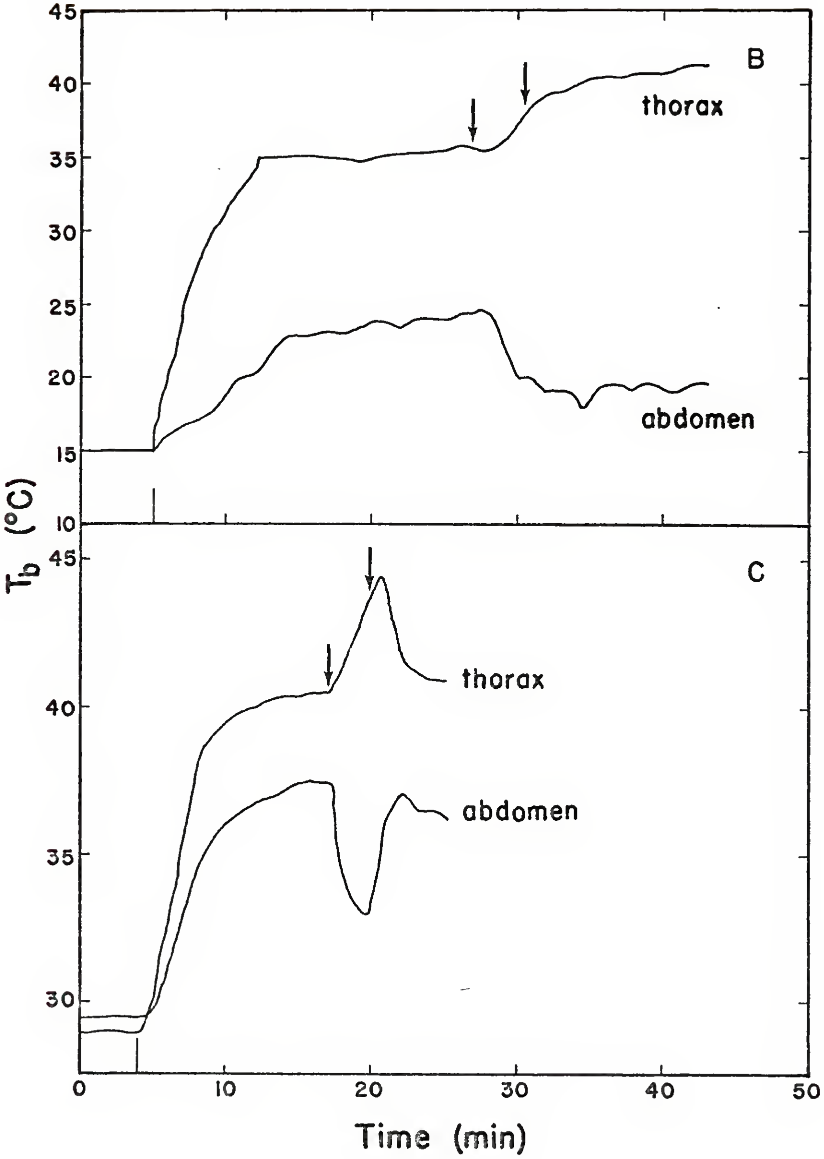

A
thorax
abdomen
thorax
abdomen
thorax
abdomen
thorax
abdomen
T_b (°C)
40
35
30
25
20
15
40
35
30
25
20
15
0
10
20
30
0
10
20
30
40
Time (min)

Figure 25B. As in A, in a female *Anax* at T_a = 15°C. Note the very sharp reduction in the rate of increase of thoracic temperature at 35°C.

Figure 25C. As in A, in a female *Anax* at T_a = 29°C. Note that in this case thoracic and abdominal temperature nearly recovered their initial values after the abdominal clamping was released.


B
thorax
abdomen
C
thorax
abdomen
T_b (°C)
Time (min)
45
40
35
30
25
20
15
10
45
40
35
30
0
10
20
30
40
50

according to the Van't Hoff rule. When the base of the abdomen was pinched, thoracic temperature rapidly increased by 3-4°C while abdominal temperature fell sharply. Sometimes thoracic and abdominal temperature returned to near their former levels when the abdomen was released, but in other cases the temperatures did not return, probably due to structural injury of the circulatory system.

Additional evidence indicates that circulation to the abdomen is controlled. During wing-whirring, abdominal temperature increases much less than thoracic temperature and the onset of its rise is usually delayed relative to the beginning of thoracic warming (Figure 26). Sometimes, as in Figure 26A, abdominal temperature does not rise until after take-off. At other times there is less delay in the increase in abdominal temperature (Figure 26B), but it is usually well marked.

Another avenue of heat loss that offers some potential for control is direct convective heat loss from the thorax. Heinrich (1972e) showed that control of convection may be important in some butterflies. The cooling constant of dead *Anax* depends upon air speed (Figure 27). Heat loss at a speed of 4 m/sec is about twice that in still air; the further increase at higher velocities is slight. *Anax* occasionally hovers, so its air speed probably can vary from 0 to 8 or 9 m/sec (Corbet, 1963). Thus this species, and others as well, could exert some control of heat loss by varying air speed. However, although flight speed is difficult to estimate accurately, there is no obvious alteration of speed in response to temperature. Dragonflies do not appear to fly slowly at low T_a and faster at high T_a. Increased

Figure 26A. A direct tracing from a recording of thoracic and abdominal temperature during wing-whirring and subsequent cooling in a female *Anax*. The thermocouple junction was in the third abdominal segment T_a = 20°C.

Figure 26B. As in A, in a second female specimen. The junction was in the second abdominal segment.

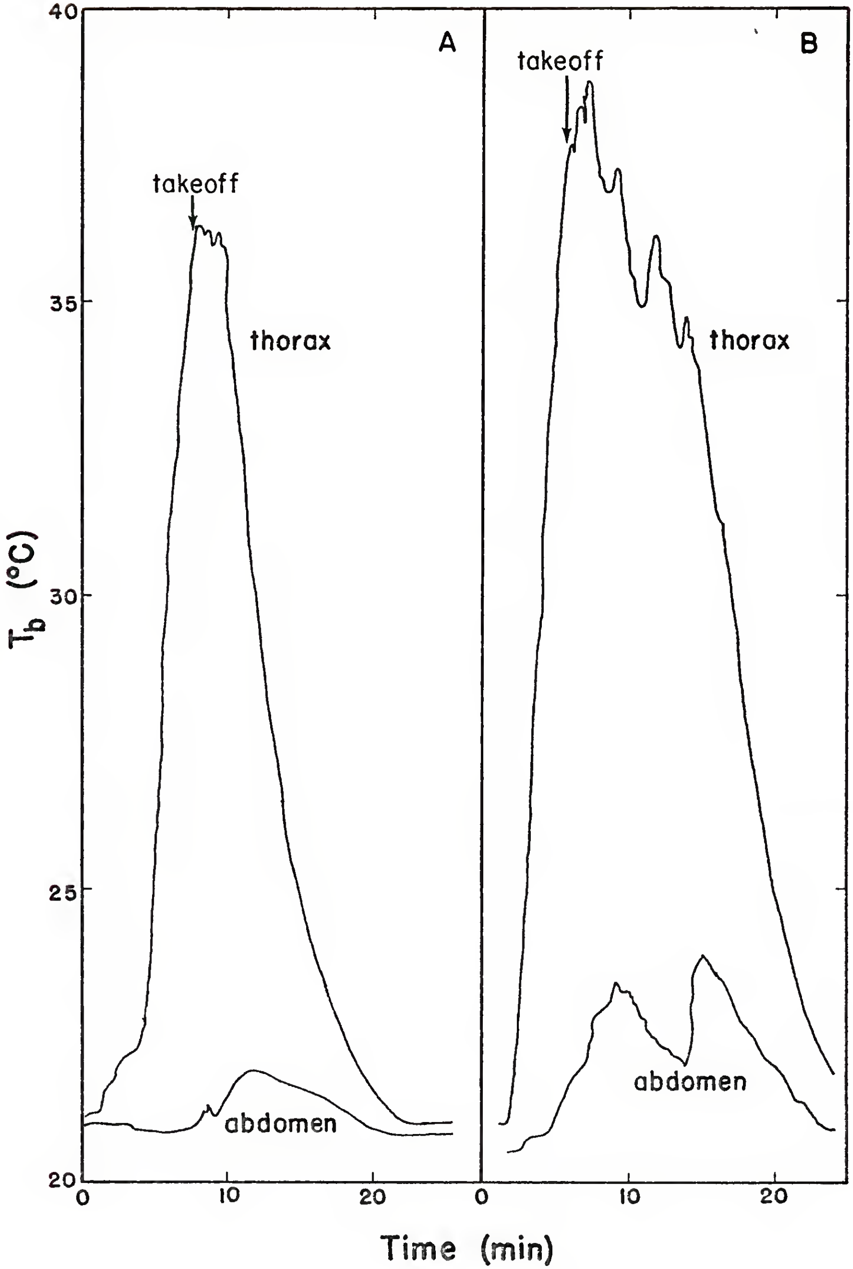
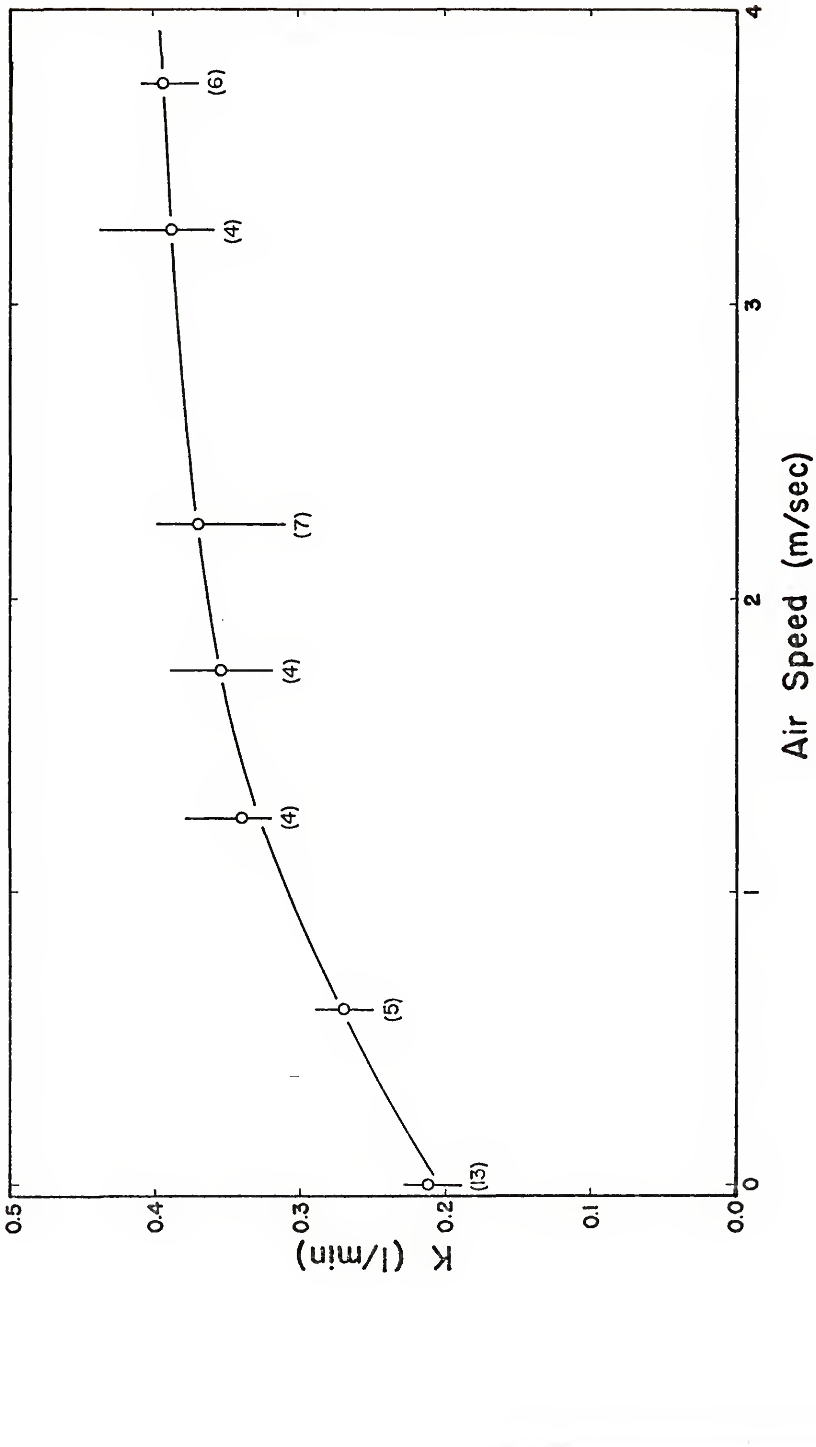

A
B
takeoff
takeoff
thorax
thorax
abdomen
abdomen
T_b (°C)
40
35
30
25
20
0
10
20
0
10
20
Time (min)

Figure 27. Cooling constant as of function of air speed in *Anax junius*. Circles indicate the mean, vertical lines the range at each speed. Numbers in parenthesis are the number tested at each speed.


K (l/min)
0.0
0.1
0.2
0.3
0.4
0.5
Air Speed (m/sec)
0
1
2
3
4
(13)
(5)
(4)
(4)
(7)
(4)
(6)

convective heat loss does occur during fast powered flight, such as chases among males, and may be important in passively dissipating some of the additional heat produced then.

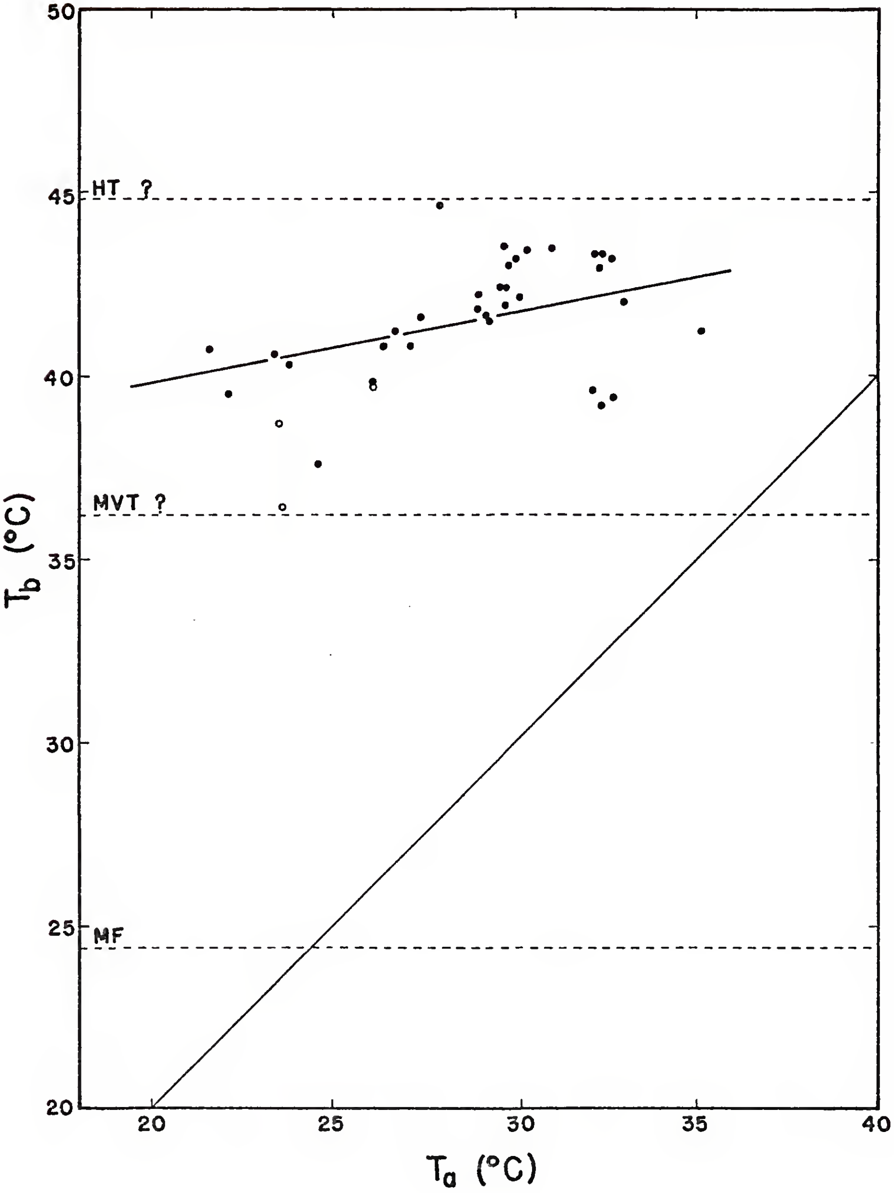
Macromia taeniolata

This very large flier is taxonomically rather close to the Libellulidae but behaviorally more like an aeshnid. It is an excellent thermoregulator, as shown in Figure 28 and Table 4. The regression line does not include the few data on females, which seem to be consistently lower than males. All of the males were taken while patrolling a large, sunny stream near Gainesville. Among the dragonflies considered here, this species is the best regulator of T_b in terms of the ratio, $\Delta T_b/\Delta T_a$. It also has the highest T_b.

The mechanisms of T_b control are something of a mystery. *Macromia* warms up effectively. Heat production is not as rapid as in *Anax* (Table 10) but the cooling constant is low and differentials between T_b and T_a as large as 23°C during warm up and 19°C during flight have been measured. During patrol flights at all temperatures, short periods of flapping alternate with periods of gliding. At low T_a the glides are short while at high T_a in direct sunlight they may last several seconds; gliding never predominates to the extent that it does in *Tramea*. This is one of the few species observed wing-shivering in the field. A female that had been knocked into the water flew to a bridge piling and wing-whirred briefly before taking off.

Little change of cooling constant with temperature occurs (Figures 30-33 and Table 8). A single experiment run with the abdomen free or clamped off at the base indicated no marked effect of abdominal

Figure 28. Relation of T_b to T_a in free-ranging *Macromia taeniolata*. Symbols as in Figure 23. The regression line refers to males only.


50
45
40
35
30
25
20
HT ?
MVT ?
MF
T_b (°C)
20
25
30
35
40
T_a (°C)

circulation on conductance. While these few data do not rule out the possibility of heat loss via the abdomen, they certainly suggest that it is less important than in *Anax*. The possibility of direct control of convection from the thorax by varying air speeds exists here, but, as in *Anax*, there is no indication that flying speed depends on T_a.

Macromia does exhibit a type of behavior that is rarely seen in *Anax* and which could have great consequences for thermoregulation. From time to time flying individuals will hit the water, submerging their body almost completely and sometimes wetting their wings. This must reduce T_b, both by the immediate conduction of heat to the water (water temperature is generally around 26°C at this site) and by evaporative heat loss over the next few minutes. However, this activity may occur before sunrise and throughout the morning. It seems to be more common during hotter periods, but the correlation with temperature is poor. Corbet (1963) briefly reviewed information on similar incidents in other species and concluded that striking the water is usually accidental.

Since these dragonflies are quite large and are very dark, they might gain more heat from incident insolation than other species (see p. 201). As with the other species there appears to be no alteration of flight direction in response to sunlight and temperature. *Macromia* tends to follow landmarks at all times of day. They may tend to avoid bright sunlight at high T_a; however, quantitative data are lacking. The stream where they were collected is broad and open. About 50 meters downstream it narrows and is largely shaded by over-hanging trees. On very hot days, few or no *Macromia* fly in the open in early or midafternoon although they are abundant there earlier in the day. Downstream, however, a few individuals may be seen still patrolling in or near the shaded stream. These odonates evidently reduce activity or transfer it to cooler habitats at high temperatures. A similar pattern of behavior was noted by Robert (1958) in *Aeshna cyanea*, and Paulson (pers. comm., 1973) has noted that *A. multicolor* reduces activity and seeks shelter under the same conditions. Nevertheless, flying in the shade can hardly account for the thermoregulatory ability of *Macromia* because they are active at T_a as high as 31-33°C and as low as 21°C, but the expected T_b varies only from 40°C to 42°C over this range.

Miscellaneous Observations

During the course of this investigation I have had the opportunity to observe many other species. It is obvious that posture plays a role in the thermal relations of many dragonflies. Table 6 summarizes data on the use of the obelisk posture.

The taxonomic distribution of the species in Table 6 is hardly random, but there seems to be no overall pattern in the occurrence of the obelisk. Both suborders of Odonata are represented, if the *Calopteryx* record is accepted, as are both the major families of perchers among the Anisoptera and several different subfamilies within these families. It appears likely on this evidence that the obelisk posture has evolved several times as a natural consequence of the perching habit and the elongate odonate body form.

Table 6. Species known to employ obelisk posture.

Family	Subfamily[a]	Species	Source
Gomphidae	Gomphinae	*Gomphus cavillaris*[b]	pers. obs.
	Gomphoidinae	*Aphylla williamsoni*	pers. obs.
Libellulidae	Tetratheminae	*Nannothemis bella*[b]	pers. obs.
	Diastatopidinae	*Perithemis tenera*[b]	pers. obs. & Hardy, 1966
	Brachydiplactinae	*Micrathyria* sp.[c]	pers. obs. & Paulson, 1966
	Sympetrinae	*Crocothemis erythraea*	Corbet, 1963
		Diplacodes sp.	Corbet, 1963
		Erythemis peruviana	Needham & Westfall, 1955
		Erythrodiplax connata[b]	pers. obs.
		E. berenice	pers. obs.
		Pachydiplax longipennis[b]	pers. obs., & others
	Leucorrhinae	*Brachymesia gravida*[b]	pers. obs. & Paulson, 1966
		Celithemis amanda	pers. obs.
		C. elisa	pers. obs.
		C. fasciata	pers. obs.
		C. ornata	pers. obs.
	Tritheminae	*Trithemis festiva*	Corbet, 1963
	Pantalinae (= Trameinae)	*Idiataphe* sp.	Paulson, 1966
	unclassified	*Dythemis multipunctata*[d]	pers. obs.
		Macrodiplax balteata[e]	pers. obs.
Calopterygidae		*Calopteryx maculata*	pers. obs.
		Hetaerina americana	Johnson, pers. comm., 1973

[a] classified according to Fraser (1957).

[b] tested by varying exposure to sun and shade.

[c] apparently without thermoregulatory significance; see text.

[d] not listed in Fraser (1957). The obelisk posture was seen only in the laboratory, although this species often perches with a moderately elevated abdomen in the field.

[e] Fraser's (1957) classification incorrect (Paulson, 1966).

The single observation of *Calopteryx maculata* in an obelisk is highly unusual and for two reasons is somewhat suspect. It is the only time I observed a damselfly apparently adjusting its posture in response to sunlight. The related species, *Hetaerina americana*, probably does so also (Johnson, pers. comm., 1973). *Calopteryx* frequently bends its abdomen upward in sexual displays that expose a white area on the tip of the abdominal venter (Johnson, 1962a). However, this specimen was perched quietly on a stem with no other individuals in the immediate area. It did not alter its posture when approached, but it did partly lower its abdomen when shaded with an insect net. When a cloud obscured the sun it lowered its abdomen fully, raising it again with the sun reappeared.

Field data are at hand for three related tropical species, *Micrathyria eximia*, *M. aequalis*, and *M. ocellata*. These data will not be presented in detail since several aspects of their thermal relations require more data and analysis to understand. However, two points are worth mentioning. These are all fairly small dragonflies and are perchers. Although the data extend over a range of T_a of about 10°C and show relatively little scatter, no evidence of heliothermic regulation of T_b and no correlation between posture and temperature exists. However, there may be a correlation between body size and the lower limit of T_a for activity. *Micrathyria ocellata* (0.08 - 0.12 g) appears at breeding sites before sunrise and can maintain T_b 10°C above T_a by continuous flight. *Micrathyria aequalis* (0.07 - 0.10 g) becomes active about the time that sunlight becomes available and *M. eximia* (0.04 - 0.06 g) appears somewhat later still.

A larger species, *M. atra* (0.17 - 0.23 g) seems to inhabit shaded areas primarily.

No evidence suggests that species of *Micrathyria* alter their posture in response to temperature or sunlight. They often perch with abdomens erect, as in the obelisk posture. However, this behavior occurs under a variety of environmental conditions, and it seems to be exclusively for the purpose of displaying the light markings that occur on the distal abdominal segments of males. These insects do not use the obelisk as a means of preventing overheating in the laboratory.

DISCUSSION

Thermal Conductance

Thermal conductance measures the ease of heat exchange between a body and its environment by conduction, convection, and radiation. Conductance may be derived from the cooling constant, K, associated with Newtonian cooling, *i.e.*, $dT_b/dt = K(T_b - T_a)$, where temperature is measured in °C, t in minutes, and K has units of 1/min. The cooling constant may be converted to thermal conductance, C, in units of cal/g·°C·hr, by multiplying by the specific heat of insect tissue (approximately 0.82 cal/g·°C) and by 60 to convert from minutes to hours.

Two assumptions implicit in the method of calculating K (see pp. 17-18) are that metabolic heat production and evaporative heat loss were negligible during cooling. The first of these seems reasonable since specimens hung quietly and T_b dropped to within a few tenths of a degree of T_a. Evaporative cooling was generally minimized by placing the insects in a nearly saturated atmosphere, but Table 7 shows that humidity had no effect on calculated values of K in *Tramea carolina*. Similar results were obtained in *Anax junius*. Also, Church (1960a) found that heat loss due to evaporation is small in flying insects. In similarly shaped animals K, and thus C, is a function of body size, because heat exchange depends on the surface to volume ratio and the rate of conduction from core to surface, and a function of surface-specific insulation, *i.e.*, the effect of

Table 7. Effect of humidity on cooling constant in *Tramea carolina*.

T_a	R.H.	n	Mean K ± S.D.
15°	0	5	0.29 ± 0.037
15°	100	5	0.29 ± 0.039
25°	0	5	0.32 ± 0.036
25°	100	5	0.33 ± 0.018

fur, feathers, scales, air sacs, etc. If conductance is high, heat exchange is rapid and the temperature of the animal is more tightly coupled to that of its environment. Largely for this reason, small dragonflies usually thermoregulate less well than large ones. Of course, it is possible to compensate for high conductance, but to do so requires increasing postural adjustments or heat production.

Figures 29-33 show log-log plots of K vs. thoracic weight for a number of species of Florida dragonflies, both dead and alive at various ambient temperatures. Table 8 shows mean value of K in various species as a function of T_a. The high correlation of K with thoracic weight is obvious in all the graphs. There is one aberrant point representing a *Miathyria* at T_a = 20°C. This specimen may have maintained low levels of muscular activity during cooling, but there is no direct evidence for this.

It is also apparent that dead specimens cool more slowly than live ones at any temperature, except those with very small thoracic weight, in which there is essentially no difference. This situation is in contrast to birds and mammals. For example, a comparison of the equation of Lasiewski, *et al.* (1967) for conductance in live birds with that of Herreid and Kessel (1967) for dead birds shows that the latter have about 15% higher conductance. McNab and Morrison (1963) obtained similar results with live and dead *Peromyscus*. Apparently vertebrate endotherms can decrease conductance by erecting their feathers or fur enough to compensate for the increased heat loss due to circulation in live animals. Dragonflies have no known mechanism to increase their insulation, however. They can increase their cooling constant by means of circulation to peripheral regions

Figure 29. Cooling constant as a function of thoracic weight (W) in dead temperature zone Anisoptera. The line is the least squares regression of log C on log W, and the equation is $\log C = -0.918 - 0.488 \log W$, $r - -0.9826$. The ambient temperature at which each specimen was tested is indicated as follows: + - 15°C, • - 20°C, ∘ - 25°C.

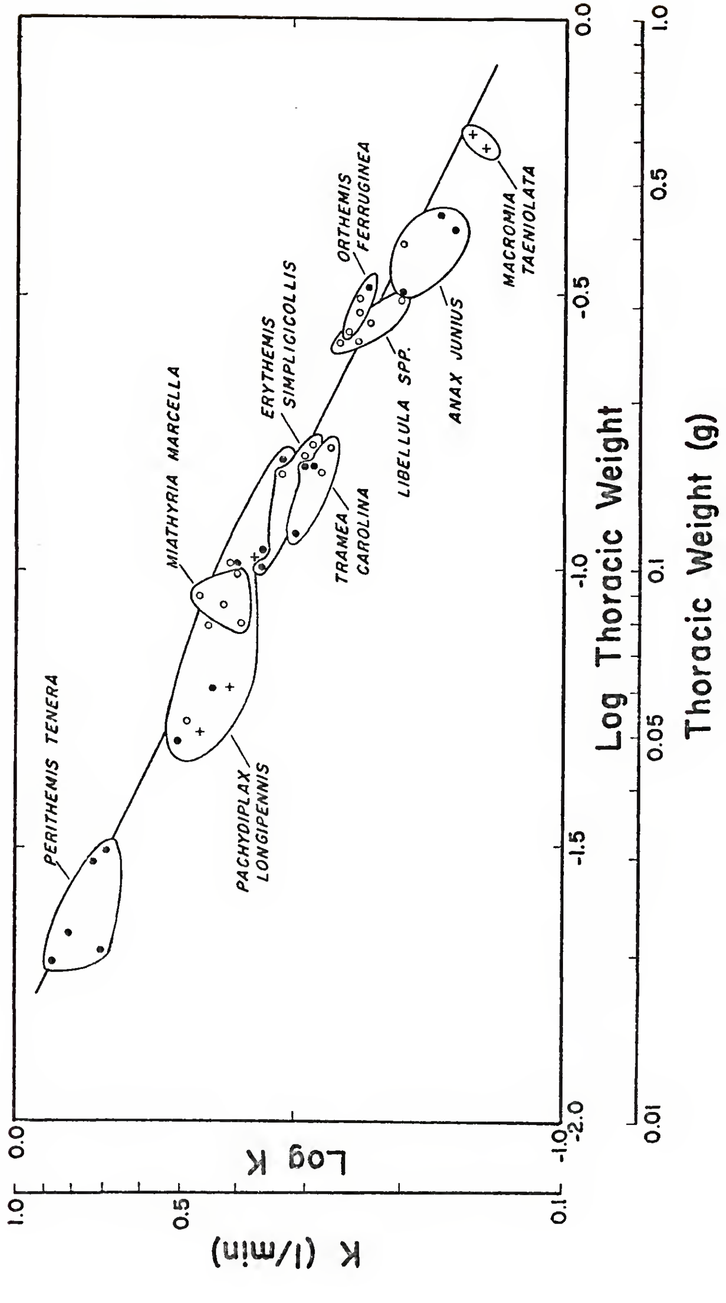
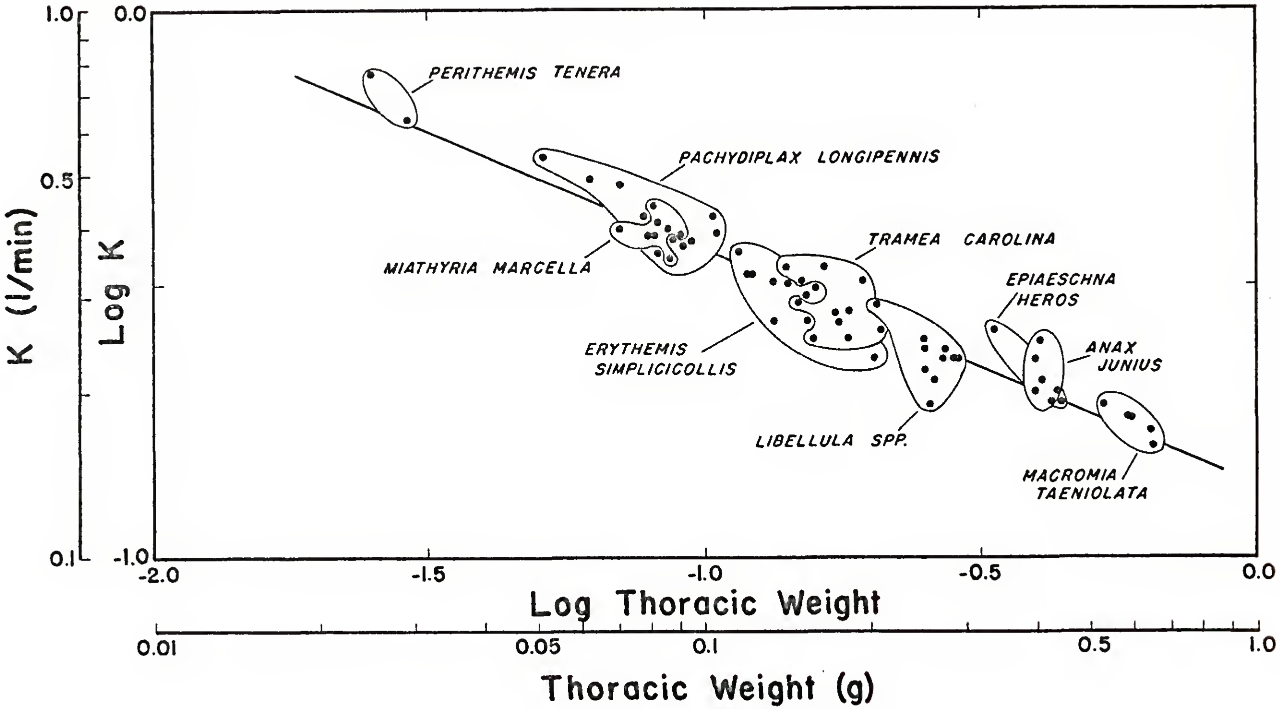
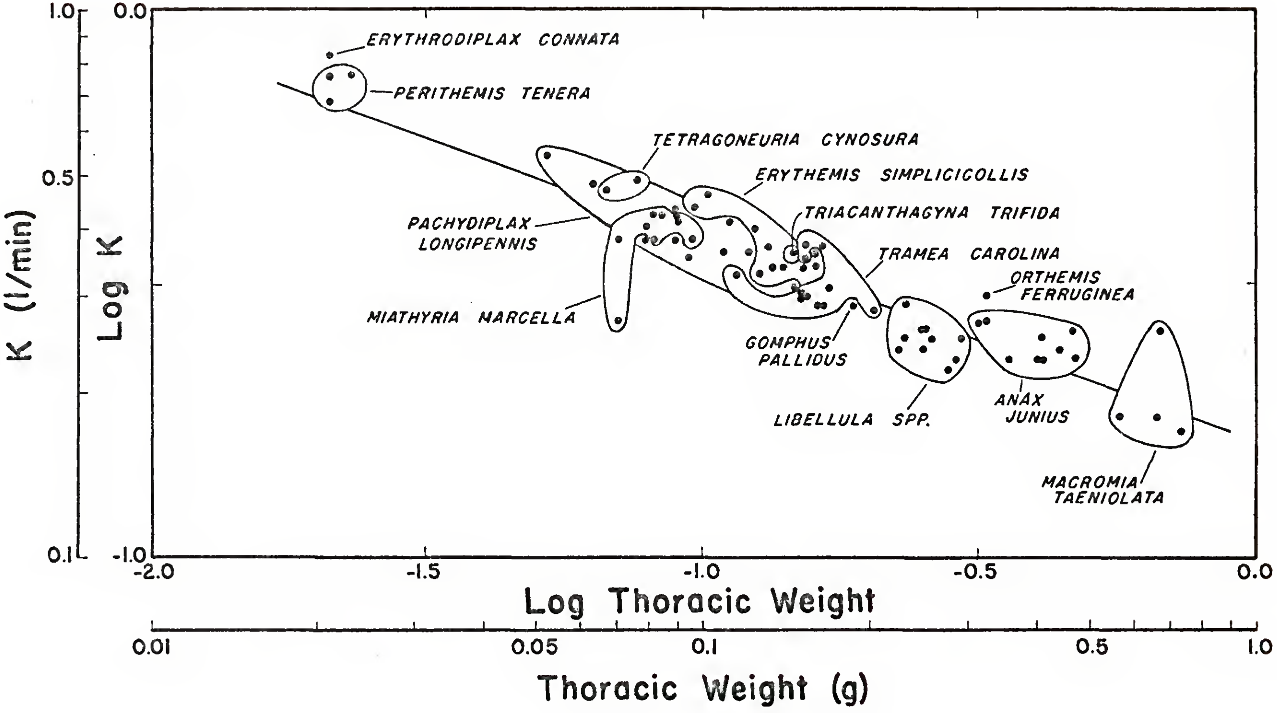

PERITHEMIS TENERA
PACHYDIPLAX LONGIPENNIS
MIATHYRIA MARCELLA
ERYTHEMIS SIMPLICICOLLIS
TRAMEA CAROLINA
LIBELLULA SPP.
ORTHEMIS FERRUGINEA
ANAX JUNIUS
MACROMIA TAENIOLATA
Log K
0.0
-1.0
K (l/min)
1.0
0.5
0.1
Log Thoracic Weight
-2.0
-1.5
-1.0
-0.5
0.0
Thoracic Weight (g)
0.01
0.05
0.1
0.5
1.0

Figure 30. Cooling constant as a function of thoracic weight in living temperate zone Anisoptera at T_a = 15°C. The least squares regression is $\log C = -0.866 - 0.432 \log W$, $r = -0.9606$.



PERITHEMIS TENERA
PACHYDIPLAX LONGIPENNIS
MIATHYRIA MARCELLA
TRAMEA CAROLINA
ERYTHEMIS SIMPLICICOLLIS
EPIAESCHNA HEROS
ANAX JUNIUS
LIBELLULA SPP.
MACROMIA TAENIOLATA
Log K
K (l/min)
0.0
-1.0
1.0
0.5
0.1
-2.0
-1.5
-1.0
-0.5
0.0
Log Thoracic Weight
0.01
0.05
0.1
0.5
1.0
Thoracic Weight (g)

Figure 31. Cooling constant as a function of thoracic weight in living temperate zone Anisoptera at T_a = 20°C. The least squares regression is log C = -0.790 - 0.377 log W, r = -0.9325.



ERYTHRODIPLAX CONNATA
PERITHEMIS TENERA
TETRAGONEURIA CYNOSURA
ERYTHEMIS SIMPLICICOLLIS
TRIACANTHAGYNA TRIFIDA
PACHYDIPLAX LONGIPENNIS
TRAMEA CAROLINA
ORTHEMIS FERRUGINEA
MIATHYRIA MARCELLA
GOMPHUS PALLIDUS
LIBELLULA SPP.
ANAX JUNIUS
MACROMIA TAENIOLATA
K (l/min)
1.0
0.5
0.1
Log K
0.0
-1.0
-2.0
-1.5
-1.0
-0.5
0.0
Log Thoracic Weight
0.01
0.05
0.1
0.5
1.0
Thoracic Weight (g)

Figure 32. Cooling constant as a function of thoracic weight in living temperate zone Anisoptera at T_a = 25°C. The least squares regression is log C = 0.790 - 0.377 log W, r = 0.9293. The dashed line indicates the regression of data when *Anax junius* is not included. The equation is log C = -0.803 - 0.406 log W, r = -0.9440.

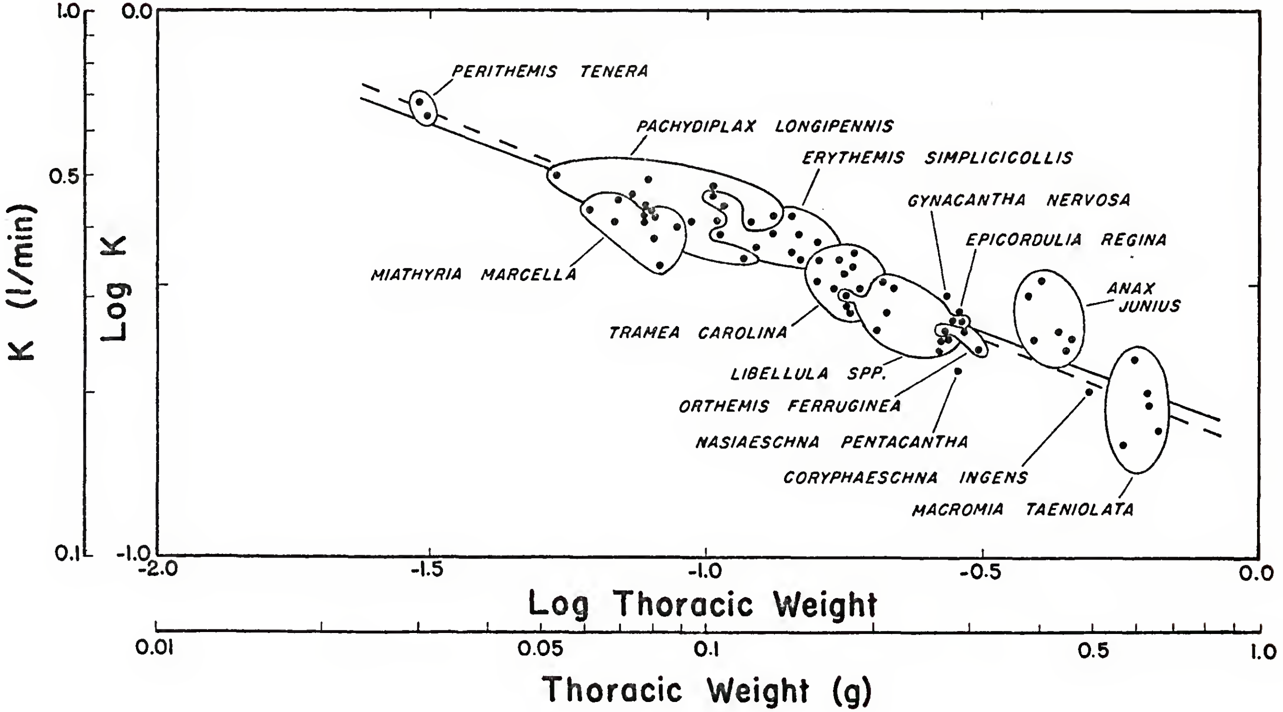

PERITHEMIS TENERA
PACHYDIPLAX LONGIPENNIS
ERYTHEMIS SIMPLICICOLLIS
GYNACANTHA NERVOSA
EPICORDULIA REGINA
ANAX JUNIUS
MIATHYRIA MARCELLA
TRAMEA CAROLINA
LIBELLULA SPP.
ORTHEMIS FERRUGINEA
NASIAESCHNA PENTACANTHA
CORYPHAESCHNA INGENS
MACROMIA TAENIOLATA
K (l/min)
1.0
0.5
0.1
Log K
0.0
-1.0
-2.0
-1.5
-1.0
-0.5
0.0
Log Thoracic Weight
0.01
0.05
0.1
0.5
1.0
Thoracic Weight (g)

Figure 33. Cooling constant as a function of thoracic weight in living temperate zone Anisoptera at T_a = 30°C. The least squares regression is log C = -0.729 - 0.341 log W, r = -0.9184.

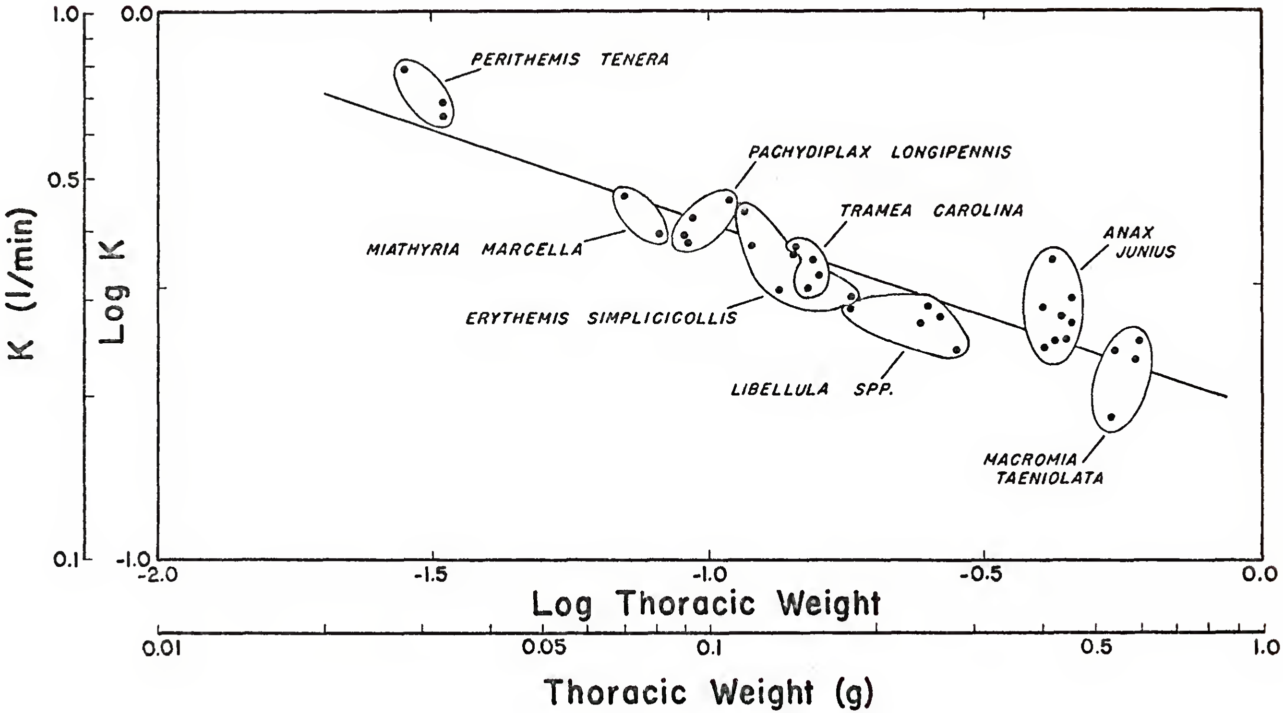

PERITHEMIS TENERA
PACHYDIPLAX LONGIPENNIS
TRAMEA CAROLINA
MIATHYRIA MARCELLA
ANAX JUNIUS
ERYTHEMIS SIMPLICICOLLIS
LIBELLULA SPP.
MACROMIA TAENIOLATA
K (l/min)
1.0
0.5
0.1
Log K
0.0
-1.0
-2.0
-1.5
-1.0
-0.5
0.0
Log Thoracic Weight
0.01
0.05
0.1
0.5
1.0
Thoracic Weight (g)

Table 8. Cooling constants of principal temperate zone species.

Species		Dead	15°C	20°C	25°C	30°C
Anax junius	N	21	25	9	14	8
	Mean	0.22	0.23	0.25	0.29	0.28
	± S.D. (1/min)	± 0.035	± 0.030	± 0.017	± 0.032	± 0.035
	Mean Wt. Thorax (g)	0.317	0.381	0.395	0.399	0.424
Erythemis simplicicollis	N	4	10	10	10	5
	Mean	0.32	0.30	0.37	0.39	0.35
	± S.D.	± 0.032	± 0.037	± 0.044	± 0.035	± 0.052
	Mean Wt. Thorax (g)	0.145	0.142	0.126	0.130	0.138
Libellula spp.	N	4	10	10	10	5
	Mean	0.23	0.23	0.25	0.28	0.27
	± S.D.	± 0.024	± 0.026	± 0.017	± 0.026	± 0.020
	Mean Wt. Thorax (g)	0.275	0.259	0.256	0.239	0.241
Macromia taeniolata	N	2	5	4	5	4
	Mean	0.15	0.18	0.20	0.19	0.22
	± S.D.		± 0.010	± 0.041	± 0.026	± 0.030
	Mean Wt. Thorax (g)	0.607	0.612	0.656	0.611	0.565
Miathyria marcella	N	4	8	9	10	2
	Mean	0.42	0.40	0.39	0.41	0.42
	± S.D.	± 0.035	± 0.024	± 0.047	± 0.030	
	Mean Wt. Thorax (g)	0.083	0.083	0.082	0.076	0.076

Table 8 Continued

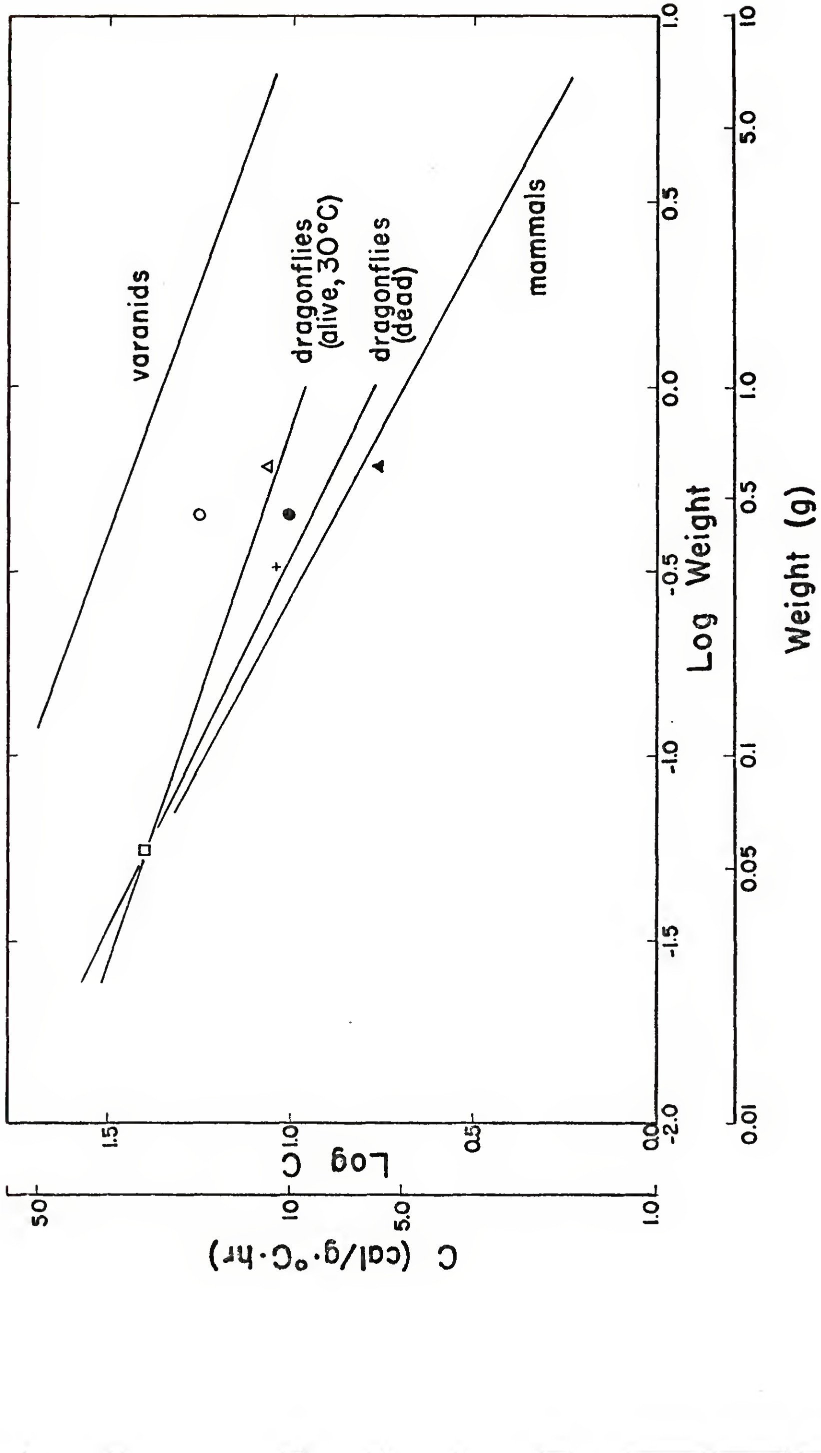
Species		Dead	15°C	20°C	25°C	30°C
Pachydiplax longipennis	N	11	10	10	10	4
	Mean	0.42	0.42	0.40	0.44	0.41
	± S.D.	± 0.055	± 0.060	± 0.068	± 0.046	± 0.032
	Mean Wt. Thorax (g)	0.084	0.082	0.095	0.095	0.095
Perithemis tenera	N	5	2	3	2	3
	Mean	0.75	0.70	0.73	0.66	0.70
	± S.D.	± 0.086		± 0.046		± 0.072
	Mean Wt. Thorax (g)	0.024	0.027	0.022	0.030	0.031
Tramea carolina	N	5	11	10	10	4
	Mean	0.29	0.29	0.31	0.32	0.34
	± S.D.	± 0.014	± 0.031	± 0.028	± 0.026	± 0.024
	Mean Wt. Thorax (g)	0.138	0.171	0.156	0.174	0.151

and, at least in theory, by increased evaporation and convective loss to tracheal air stream.

The cooling constant may be related to whole body weight, as it generally is in vertebrates, but I have chosen to use thoracic weight for two reasons. First, body weight may vary for reasons that have little relevance to K, such as loss of legs or portions of wings or the presence or absence of eggs. Second, it seems likely that only thoracic temperature is regulated. Abdominal weight may have some independent effect on K since circulation into the abdomen is important in unloading heat, but if, as I will argue (p. 139), little if any heat is stored in the abdomen, the effect should be very slight. In any case, the slope of log K vs. log body weight in dead specimens is -0.50 and in living specimens at T_a = 30°C is -0.33; both values are virtually identical to the slopes of log K vs. log thoracic weight.

Church (1960b) found that the subcuticular air sacs reduce heat loss in *Sympetrum* by about 25% and in *Aeshna* by about 50%. To get an idea of the relative effectiveness of the insulation of dragonflies, cooling constants were converted to thermal conductances, since the latter is the standard expression for vertebrate endotherms. The results appear in Figure 34. Minimal conductance in dragonflies is essentially equal to values predicted for mammals of a similar size by extrapolating the Herreid and Kessel (1967) equation for conductance in small mammals. Dragonflies have conductances far below those predicted for lizards by the equation of Bartholomew and Tucker (1964); however, the Bartholomew and Tucker equation applies to live lizards in which C is about 30% higher than in dead ones (Bartholomew

Figure 34. Thermal conductance as a function of weight in varanids (log C = 1.35 - 0.37 log W; Bartholomew and Tucker, 1964), mammals (log C = 0.69 - 0.51 log W; Herreid and Kessel, 1967), dead dragonflies (log C = 0.77 - 0.49 log W; present study), living dragonflies at T_a = 30°C (log C = 0.69 - 0.039 log W; present study), and in other insects. Note that the units of conductance are changed from previous graphs to facilitate comparison with other groups. Symbols are as follows: □ - *Bombus terricola* alive, (Heinrich, 1972); + - *Celerio lineata,* alive (Heath and Adams, 1969); Δ - *Sphinx ligustri*, dead, air speed 3.0 m/sec., thoracic weight estimated from thoracic dimensions (Church, 1969b); ▲ - *Sphinx ligustri*, corrected to expected value in still air by means of relation found by Heinrich (1971a); ∘ - *Anax imperator,* dead, air speed 2.5 m/sec., thoracic weight assumed same as *A. junius* (Church, 1960b) • - *Anax imperator* corrected to expected value in still air according to Figure 28.


varanids
dragonflies (alive, 30°C)
dragonflies (dead)
mammals
Log Weight
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
Weight (g)
0.01
0.05
0.1
0.5
1.0
5.0
10
Log C
0.0
0.5
1.0
1.5
C (cal/g·°C·hr)
1.0
5.0
10
50

and Tucker, 1963). Nevertheless, even live dragonflies at T_a = 30°C are closer to the mammal curve than to the lizard curve.

The relative degree of insulation of dragonflies is probably actually closer to that of mammals, and further from that of lizards, than indicated by Figure 34. Very small bodies lose heat by convection more rapidly than would be predicted by the relation of heat loss to size in large bodies (see p. 201), so the conductance of an hypothetical 0.5 g mammal would actually be higher than predicted by linear extrapolation of the Herreid and Kessel curve.

Enough data are available on a few other insects to compare with dragonflies, although some uncertainty exists in estimating thoracic weight and the effect of wind speed for the data from Church (1960b). Close agreement appears between the data on dragonflies and those on endothermic insects in other orders (Figure 34). Sphinx moths probably have slightly better insulation than dragonflies, bees about the same, but all these groups are close to the mammal curve.

Besides body size, the major determinant of the cooling constant is temperature. For example, a comparison of Figures 30-33 clearly shows an increase in conductance at high ambient temperatures in large individuals, but little effect in small ones. As shown for *Anax*, this is probably due to an increase in circulation from the thoracic core to peripheral areas at high temperatures. The circulatory system of dragonflies is well suited for this, since the ventral centrifugal stream of haemolymph in the abdomen is separated from the dorsal returning stream by the ventral septum (Jones, 1964). This structure would reduce heat transfer from the warm outflow to the cool inflow by preventing mixing. The elongate shape of the abdomen and comparative lack of insulating air sacs also adapts it for augmenting heat loss.

Small dragonflies show relatively little increase in conductance with an increase in T_a. This stems from the fact that heat loss in small bodies is very rapid under all circumstances. The additional heat loss resulting from rapid circulation is negligible. This analysis receives support from the fact that there is no difference in K between living and dead individuals of small species.

Invoking special circulatory mechanisms to explain the dependence of the cooling constant on temperature is not necessary. Heart rate in insects increases with temperature (Jones, 1964), and it more than doubles between 15°C and 30°C in *Periplaneta americana* (Richards, 1963). Therefore, the rate of circulation probably increases with temperature, resulting in faster transfer of heat between body and environment. On the other hand, living *Anax* consistently have cooling constants higher than expected for other species, especially at high ambient temperatures. This observation coupled with evidence that control of circulation to the abdomen is under voluntary control in this species leads to the conclusion that *Anax* selectively shunts blood to the abdomen or controls stroke volume (McCrea and Heath, 1971) at high temperatures.

For the data on conductance change it is possible to estimate the rate of circulation necessary to account for the additional heat loss in *Anax*. Since

$$\Delta(dH/dt) = \Delta C(T_b - T_a)$$

$$\Delta(dH/dt) = (0.26\ \text{cal/g}\cdot{}^\circ\text{C}\cdot\text{min})\ (T_b - T_a)$$

Assume that the hemolymph has the specific heat of water (1.0 cal/g·°C), and that all heat entering the abdomen dissipates to the air. The latter assumption cannot be exactly true, but given the attenuated abdomen of dragonflies it may be nearly so. Then

$$\Delta(dH/dt) = (\text{volume circulated} \times 1.0\ \text{cal/g}\cdot{}^\circ\text{C})(T_b - T_a)$$

$$0.26\ \text{cal/min}\cdot{}^\circ\text{C}(T_b - T_a) = (\text{volume circulated} \times 1.0\ \text{cal/g}\cdot{}^\circ\text{C})(T_b - T_a)$$

$$\text{volume circulated} = 0.26\ \text{ml/min}$$

This value may be compared to the maximum value of 0.4 ml/min calculated for *Manduca sexta* (McCrea and Heath, 1971).

The results presented here may underestimate the possible change in heat loss in the field for two reasons. First, in the specimens used in conductance studies the abdomen was heated to about the same initial temperature as the thorax, so heat transfer from the thorax to the abdomen must have been impeded. The importance of this factor depends on the quantity of heat stored in the abdomen, apparently a small amount. The conductance of the abdomen in dead specimens was much higher than that of the thorax. Also, no difference appeared in the thoracic conductance of individuals heated externally and those which warmed up by wing-shivering. Evidently the abdomen serves primarily as a conductor of heat from thorax to air rather than as a heat sink itself.

The second reason for underestimating the change in heat loss may be quite significant. Since the abdomen is much longer and more slender than the thorax and is uninsulated, forced convection will increase the absolute rate of heat loss from the abdomen much more rapidly than from the thorax. Thus in flight a dragonfly can probably unload much more heat by rapid circulation to the abdomen than it can in still air.

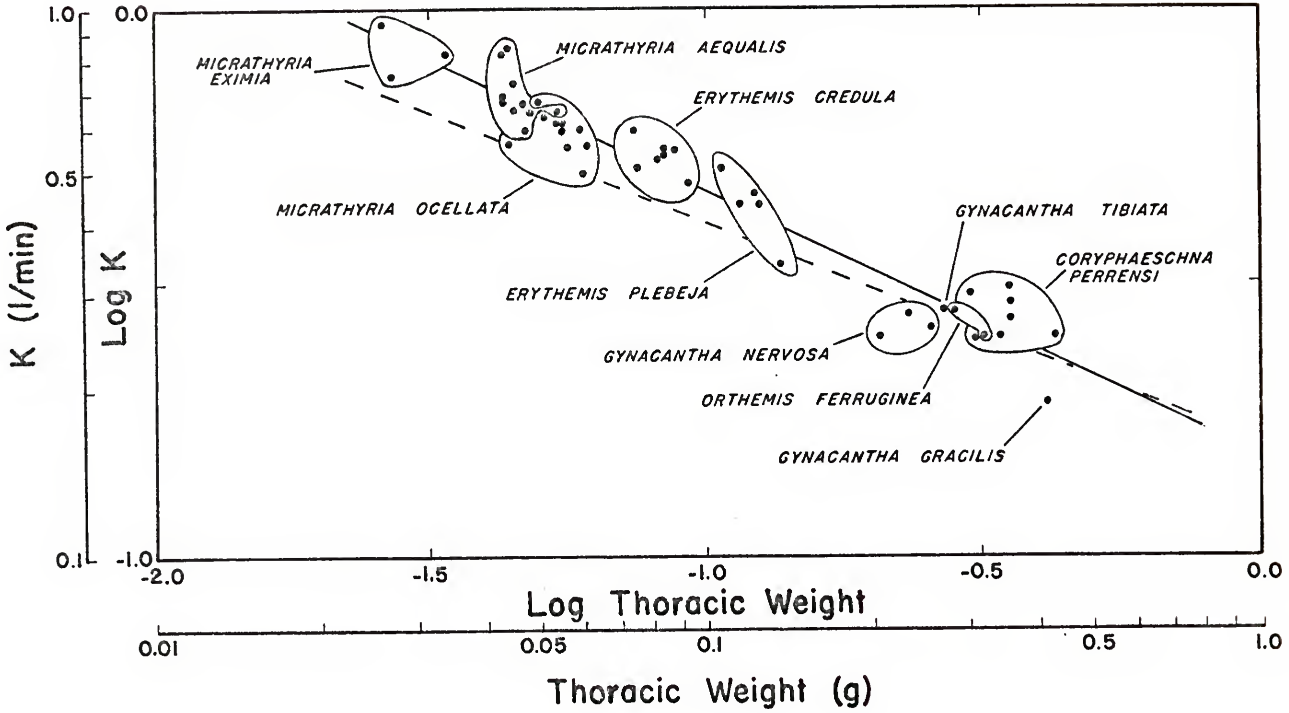
Control of circulation to other parts of the body could also contribute to temperature regulation. Hankin (1921) mentions that trameines flying with depressed abdomens may also partially extend their wings, and this is a conceivable route of heat loss. Circulation to wings also occurs, since drops of haemolymph form at the cut ends of major wing veins (and see Jones, 1964). The wings would be ideal for dissipating heat because of their high surface to volume ratio. However, resistance to blood flow must be very high. The major wing veins appear to have lumens of about 10^{-2} cm diameter, but blood probably returns via the much smaller posterior veins (Jones, 1964) which probably have lumen diameters about a tenth of this. Assuming that lumen diameters are 10^{-2} cm, that the viscosity of haemolymph is about twice that of water, and that haemolymph pressure during flight is about 2 dynes/cm^2, probably a large overestimate (Jones, 1964), then by Poiseuille's equation, $V/t = \frac{\pi Pr^4}{8\ \ell\eta}$, the flow rate would be on the order of 10^{-4} ml/min. This value is less than 0.1% that calculated for the abdomen. Besides, reducing abdominal circulation without interfering with alar circulation completely abolishes the increase in conductance at 35°C.

While the adaptive significance of a positive dependence of conductance on temperature should be obvious for species that depend primarily on endogenous heat production, it may not be so evident for heliotherms. Species that depend on an external heat source might be expected to heat faster at higher temperatures. However, the behaviors used to decrease solar heat input, specifically the obelisk and the use of perches on the shaded side of the narrow stems, actually reduce the exposed surface of the abdomen relatively more than that of the thorax. Also, convective heat loss from the abdomen is higher. This means that the effective temperature to which the abdomen is exposed is generally less than that to which the thorax is exposed, so increased circulation to the abdomen results in greater heat loss, an advantage during heat stress.

There is no evidence that factors other than body weight and temperature have systematic effects on conductance in temperate zone Odonata. In particular it does not seem that fliers and perchers differ in conductance in ways that cannot be explained by these two factors. Aeshnids, except *Anax*, do not seem to have consistently different values from other groups, and no other taxonomic correlations are evident.

Figure 35 shows a log-log plot of K vs. thoracic weight for live tropical dragonflies at T_a = 25°C. The cooling constant is higher in tropical species at thoracic weights below about 0.5 g but is slightly higher in species from Florida at higher weights. The slope is identical to that for dead temperate zone specimens, but the values are about 20% higher. Why the greatest differences exist between temperate and tropical species at the smallest weights is not clear. It was expected that any differences would be most evident at large sizes where differences in insulation and circulation could come into play. The explanation may lie in the techniques used to determine the cooling curves (see pp. 14 and 18). The method used in Panama might simply have been inaccurate at low body weights, where cooling was very rapid. Resolution of the question of the effect of climate on conductance must await further data.

Figure 35. Cooling constant as a function of thoracic weight in living tropical Anisoptera at T_a = 25°C. The least squares regression is $\log C = -0.822 - 0.488 \log W$, $r = -0.9677$. Dotted line indicates regression in temperate zone species other than *Anax* at T_a = 25°C (Figure 32).


MICRATHYRIA EXIMIA
MICRATHYRIA AEQUALIS
ERYTHEMIS CREDULA
MICRATHYRIA OCELLATA
ERYTHEMIS PLEBEJA
GYNACANTHA TIBIATA
CORYPHAESCHNA PERRENSI
GYNACANTHA NERVOSA
ORTHEMIS FERRUGINEA
GYNACANTHA GRACILIS
K (l/min)
1.0
0.5
0.1
Log K
0.0
-1.0
-2.0
-1.5
-1.0
-0.5
0.0
Log Thoracic Weight
0.01
0.05
0.1
0.5
1.0
Thoracic Weight (g)

Pre-Flight Warm-Up

The key distinction between endothermy and ectothermy is that endotherms can raise or maintain T_b far above T_a by metabolic heat production. In mammals and birds an important response to low T_a is shivering. Insects show an analogous response in warm-up by wing-whirring. Many dragonflies are capable of this behavior (Table 9). The warm-up behavior of odonates in the laboratory was essentially similar in all species examined. Sometimes warm-up began spontaneously. If not, the end of the abdomen was pinched. This usually elicited a brief bout of struggling, high amplitude wing flaps, and sometimes a brief flight if T_a was high. Then the insect commenced rapid, low amplitude wing vibrations, similar to the well known wing-shivering of sphinx moths (Dorsett, 1962). The wings might be held in any position from horizontal to nearly vertical. Usually both fore and hind wings vibrated. Wing-whirring might be continuous or interrupted at intervals of a few seconds by brief pauses. Generally no other motion of the body occurred except for occasional repositioning on the perch and intermittent eye grooming, most frequently shortly before takeoff. Takeoff rarely occurred without any break in wing movements and typically was preceded by a pause of several seconds or a bout of high amplitude flapping while still on the perch.

Not all dragonflies tested would warm up, regardless of temperature or the amount of stimulation. Some species continually tried to fly or crawl away after being pinched. Only high amplitude flapping could be elicited and this seldom lasted more than a few seconds after cessation of stimulation. When it did last longer,

Table 9. Warm-up rates and T_b at initiation of flight in Odonata; numbers in parentheses indicate number in sample.

Species	Mean Body Wt. (g)	Mean Wt. Thorax (g)	T_a (°C)	Warm-up Rate (°C/min)	T_b at Takeoff (°C)
Petaluridae					
Tachopteryx thoreyi	0.994	--	20	1.50 (1)	28.1 (1)
Cordulegastridae					
Cordulegaster sayi	0.608	--	20	2.60^a (1)	32.7 (1)
Aeshnidae					
Anax longipes	0.914	--	25	4.4 (1)	--
Coryphaeschna ingens	1.019	0.493	25	6.67 (1)	31.1 (1)
C. perrensi	0.732	0.349	25	5.3 (10)	33.8 (10)
Epiaeschna heros	0.944	0.466	15	2.15 (2)	32.9 (1)
Gynacantha gracilis	0.929	--	25	1.8 (2)	29.5 (1)
G. membranalis	0.805	--	25	3.8 (1)	30.5 (1)
G. nervosa	0.492	0.241	25	4.4 (4)	30.1 (4)
G. tibiata	0.504	0.271	25	2.5 (1)	26.9 (5)
Nasiaeschna pentacantha	0.759	0.284	25	1.52 (1)	32.9 (1)
Triacanthagyna dentata	0.562	--	25	3.8 (1)	29.8 (2)
T. trifida	0.351	0.145	20	1.48 (1)	22.5 (1)
Gomphidae					
Aphylla williamsoni	0.735	--	15	2.50 (1)	30.8 (1)
Gomphus plagiatus	0.386	--	20	3.52 (1)	29.5 (1)
Macromiidae					
Didymops transversa	0.356	--	20	5.62 (1)	35.2 (1)
Corduliidae					
Epicordulia regina	0.586	0.282	25	4.10 (1)	34.0 (1)
Somatochlora calverti	--	--	15	2.18 (1)	--
Tetragoneuria cynosura	0.150	0.072	20	2.66 (2)	--

Table 9 Continued

Species	Mean Body Wt. (g)	Mean Wt. Thorax (g)	T_a (°C)	Warm-up Rate (°C/min)	T_b at Takeoff (°C)
Libellulidae					
Miathyria marcella	0.200	0.086	15	0.89 (4)	--
Miathyria marcella	0.165	0.084	20	1.13 (5)	22.9 (2)
Miathyria marcella	0.169	0.077	25	2.72 (7)	27.1 (7)
Pantala flavescens	0.309	0.174	15	1.76 (1)	30.5 (1)

[a] maximum value, see text.

flapping was associated with crawling. These insects could raise their T_b by as much as 3-4°C if they were forced to struggle continuously, but they did not do so voluntarily.

Clearly, warm-up has a potentially profound influence on the thermal relations of dragonflies in the field. Both *Anax* and *Macromia* fly before sunrise at T_a well below their minimum flight temperature. Therefore, they must warmup before beginning to fly, although they have not been observed doing so. Caged but untethered and undisturbed individuals of another aeshnid, *Coryphaeschna perrensi*, warmed up before and just after sunrise. They took off at a mean T_b of 34.3°C (n = 7), while T_a averaged 25.8°C. Corbet (1957) noted that wing-whirring, which normally occurs in early morning, precedes the maiden flight in *Anax imperator*. Corbet and Eda (1969) saw *Anax junius* Canada flying before sunrise at a T_a of about 13°C.

Warm-up is less well developed among some trameines. *Miathyria*, in particular, warms up weakly and briefly. Its small size results in such rapid heat loss that it may have difficulty producing heat fast enough to increase its T_b much. At low T_a it seldom takes off even if wing-whirring can be elicited (Table 9). In this species the ability to warmup endothermically is probably of little importance in the field. *Tramea*, which is considerably larger, generally does warm up vigorously to takeoff at low T_a. No reliable quantitative data are available on the tropical species. Both are larger than *Miathyria*, and both can warm up by wing-shivering.

Wing-whirring was observed in the field in four species. *Macromia* has been mentioned. *Gomphus dilatatus* is a large species that alternates patrol flight with extended periods of perching. One morning before the sun had risen above the trees, an individual was observed to perch on a twig and immediately begin wing-whirring. It continued for 30-45 seconds, until disturbed. T_a was less than 25°C. Later the same day many *G. dilatatus* were active. They generally perched quietly in sunny areas. One individual perched in the shade, however, and began wing vibrations which continued with brief pauses until it took off again. I estimated T_a to be about 30°C. *Gomphus plagiatus* is a slightly smaller species and a very persistent flier for a gomphid (Paulson, 1966; and personal observations). It does perch from time to time, though, and twice I have seen it wing-whirring while perched in the shade. On other occasions specimens perched in the sun without showing warm-up behavior. Miller (1964) reported similar observations on the large African species, *Ictinogomphus ferox*. The alternate basking and wing-whirring shown by these gomphids is interesting because it seems to offer the opportunity for finer control of T_b than any studied so far. These species or similar gomphids should reward further study.

A single female *Tetragoneuria cynosura* was seen wing-whirring on a cool morning in the field. This species is about the size of *Miathyria* but warms up more strongly (Table 9).

Table 9 lists the species in which warm-up behavior was observed in the laboratory. Wing-whirring also apparently occurs in *Dromogomphus spinosus* (K. J. Tennessen, pers. comm., 1973) and *Macromia georgina* (C. Williams, pers. comm., 1973). Several tentative generalizations may be drawn from the list of species. First, warm up occurs in all families of Anisoptera. It may be universal among Aeshnidae, Macromiidae and Corduliidae, although some tropical Gynacanthaginae warm up weakly and reluctantly. All of the members of these families are fliers. Among the libellulids tested only the traimeines warm up, despite persistent efforts to prompt this behavior in *Pachydiplax, Erythemis,* and *Libellula.* On this basis one might conclude that only fliers warm up within Libellulidae. However, no data exist on libellulid fliers unrelated to the traimeines. Also, Moore (1953) reported wing-whirring in *Sympetrum striolatum*, a percher. It is not certain, however, whether he actually observed the pheonomenon or only surmised that it must take place.

Gomphidae, mostly perchers, present a varied picture. *Gomphus minutus, G. pallidus, Progomphus obscurus,* and *Epigomphus quadracies* would not warm up. *Gomphus plagiatus*, the only gomphid in my experience that might be called a flier, does warm up by wing-whirring. Among other gomphids, apparently only large species such as *Aphylla, Dromogomphus,* and *G. dilatatus* warm-up endothermically. The petalurid, *Tachopteryx*, will wing-shiver and is also a very large percher.

The occurrence of wing-shivering among distantly related taxonomic groups argues that the capability evolved several times within the Anisoptera, a conclusion in accord with the opinion of Kammer (1970) about sphinx moths.

Body temperature rises almost immediately after the insect starts wing-whirring, and the maximum warm-up rate develops quickly. The rise in T_b may continue linearly until takeoff or may decline shortly before takeoff. The latter tendency was especially true of *Tramea* at low T_a. In *Cordulegaster sayi* the rate declined continuously from the beginning of warm-up until takeoff. In all other species the linear portion was such a preponderant proportion of the entire time course of warm-up that I felt justified in using a single rate to characterize each curve. Since heat loss increases with increasing values of $T_b - T_a$, heat production must increase during warm-up. This occurs as increasing T_b results in higher muscle metabolism. Evidently the metabolic increase just balances the increase in heat loss (McCrea and Heath, 1971). Sometimes specimens would warm up but never take off. In these cases, if the individual did not simply stop wing-whirring and cool down, T_b eventually leveled off or even declined while shivering continued. In such instances the linear portion of warm-up curve was used to determine warm-up rate.

Figures 36-38 show the relation of warm-up rate and T_b at initiation of flight to ambient temperature in the species investigated intensively. The patterns of takeoff T_b show considerable variation but resemble the relations of T_b and T_a seen in the field. For instance, T_b at takeoff is virtually independent of T_a from 15°C to 25°C in female *Anax*, but within the same range it increases slightly in male *Anax*. In the field the body temperature of females is more constant than males in this ambient range. *Tramea*, which is a poor regulator, shows a marked dependence of T_b at takeoff on T_a. The high T_b recorded at T_a = 15°C probably reflects selection of especially vigorous individuals. Other specimens, which warmed up at this T_a but did not take off, did not attain such high temperatures. By contrast, the high T_b of *Macromia* at T_a = 15°C probably better represents the capacity of

Figure 36. Relation of warm-up rate (□) and T_b at initiation of flight (■) to T_a in *Tramea carolina* and *Miathyria marcella*. For *Tramea*, means are indicated by horizontal lines, ranges by vertical lines, and one standard error on either side of the mean by vertical bars. Only means of warm up rates are shown, by open circles, for *Miathyria*, because of the uncertainty of individual determinations of rate. Number in parenthesis show the number in each sample.

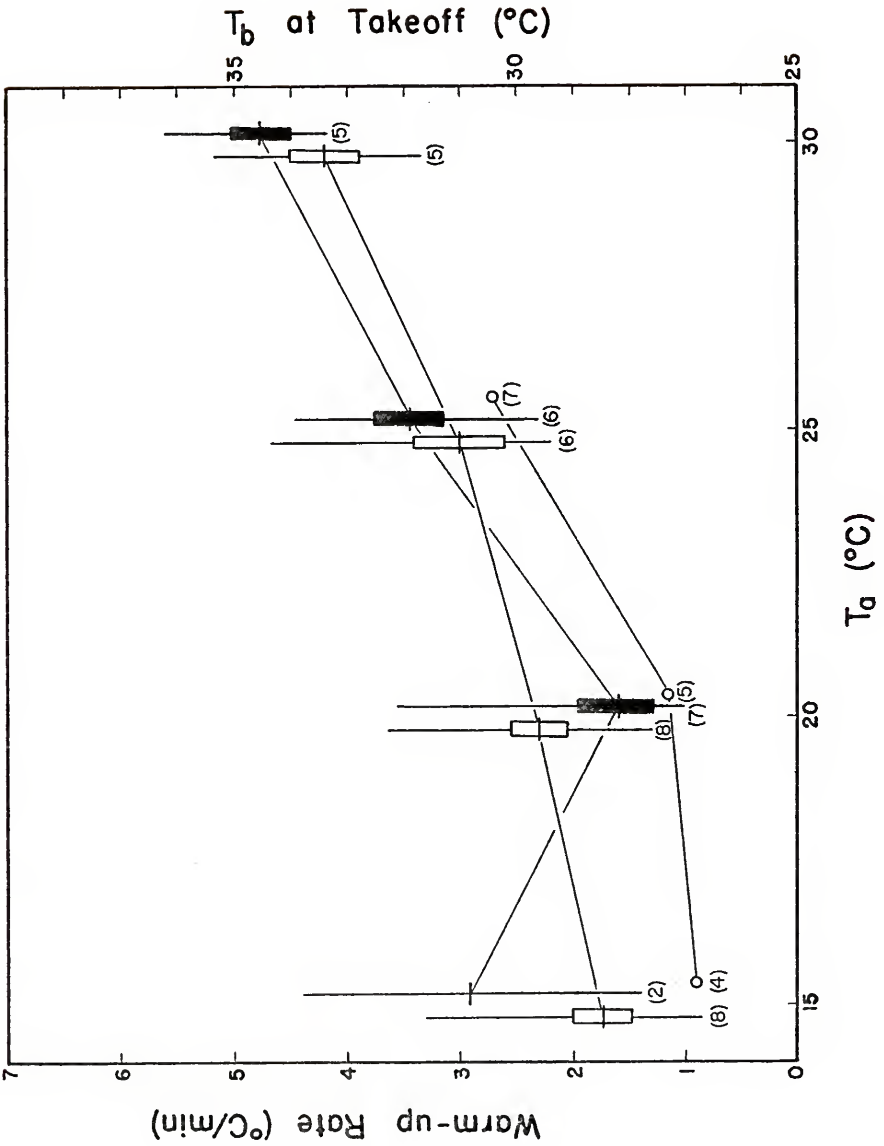

T_b at Takeoff (°C)
35
30
25
T_a (°C)
15
20
25
30
Warm-up Rate (°C/min)
0
1
2
3
4
5
6
7
(5)
(5)
(7)
(6)
(6)
(5)
(7)
(8)
(2)
(8)
(4)

Figure 37. Relation of warm-up rate and T_b at initiation of flight to T_a in *Macromia taeniolata*. Symbols as in Figure 36.

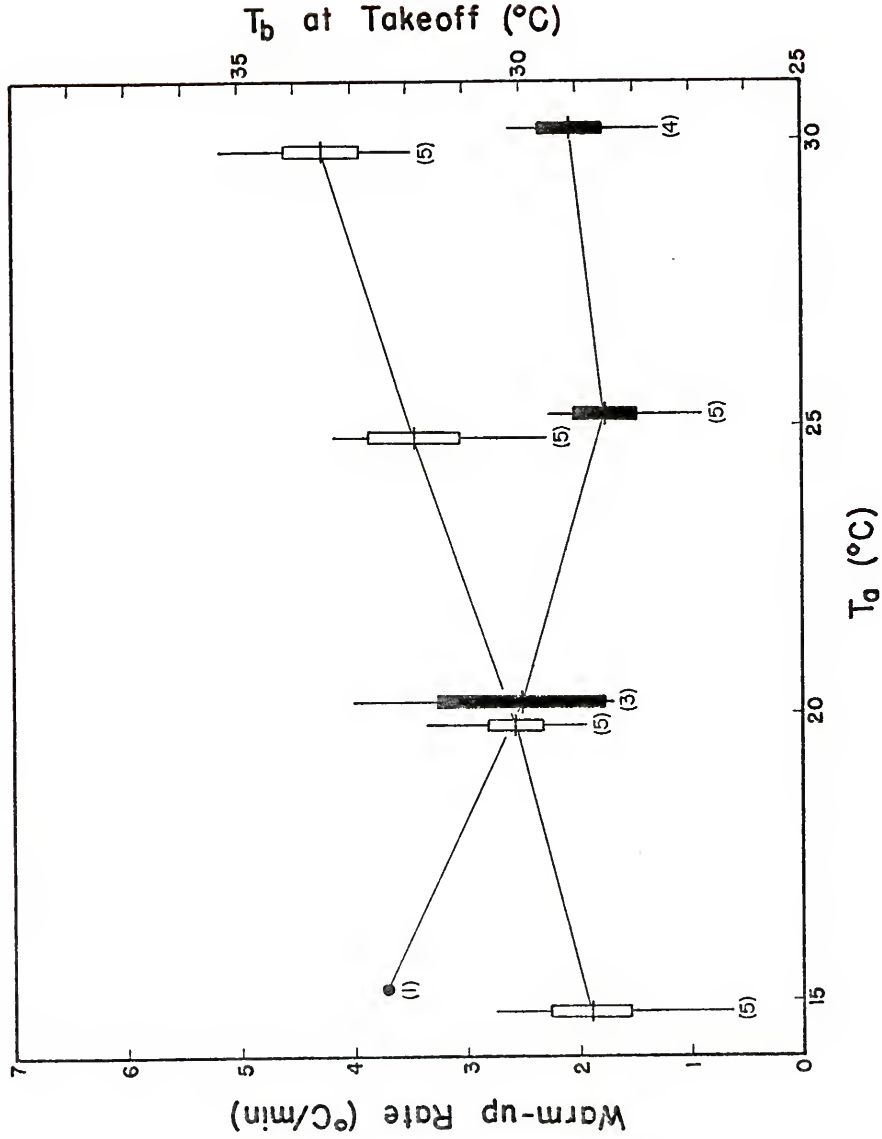

T_b at Takeoff (°C)
35
30
25
T_a (°C)
15
20
25
30
Warm-up Rate (°C/min)
0
1
2
3
4
5
6
7
(1)
(5)
(5)
(3)
(5)
(5)
(5)
(4)

Figure 38A. Relation of T_b at initiation of flight to T_a in *Anax junius* males and females. Symbols as in Figure 36.

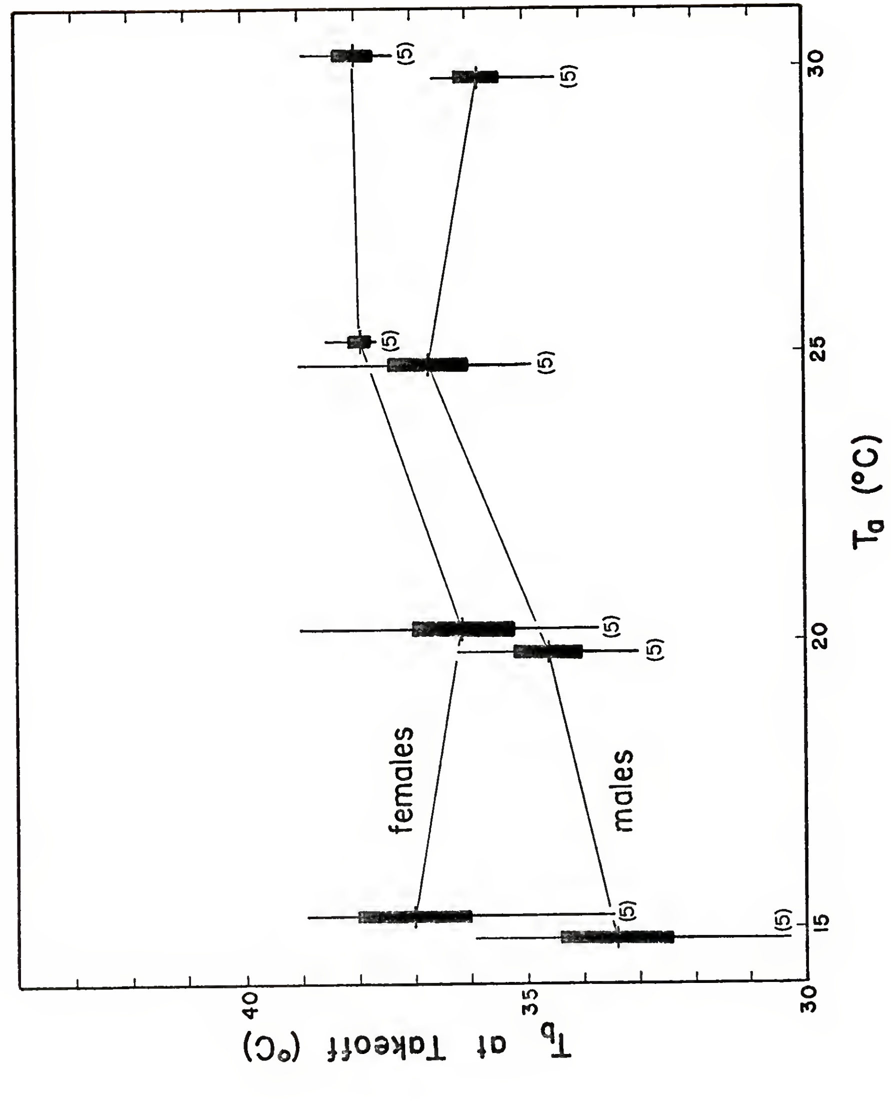
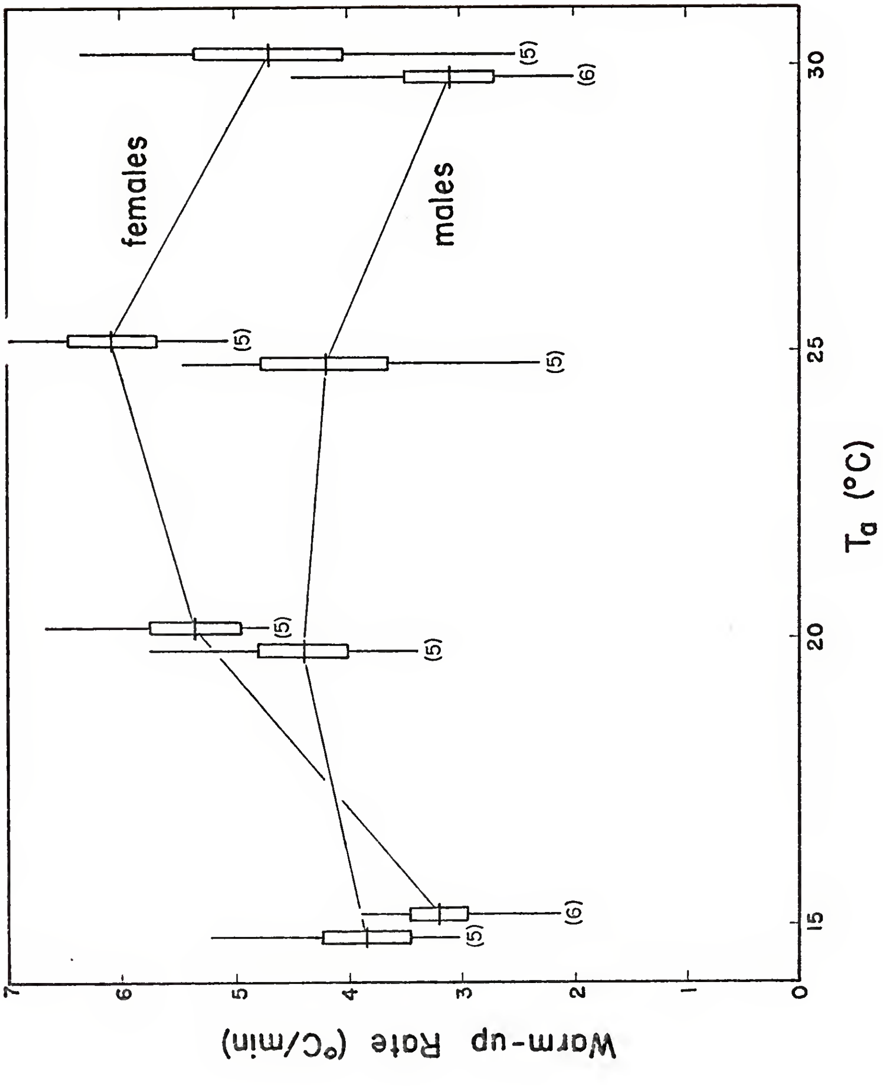

T_b at Takeoff (°C)
40
35
30
T_a (°C)
15
20
25
30
females
males
(5)
(5)
(5)
(5)
(5)
(5)
(5)
(5)

Figure 38B. Relation of warm-up rate to T_a in *Anax junius* males and females. Symbols as in Figure 36.


Warm-up Rate (°C/min)
0
1
2
3
4
5
6
7
T$_a$ (°C)
15
20
25
30
females
males
(5)
(6)
(5)
(5)
(5)
(5)
(5)
(6)

the species even though it is based on a single individual, because half the others tested attained similar T_b even though they did not fly. Both *Tramea* and *Macromia* take off at body temperatures below those generally found in the field at the same T_a. This implies that warming continues after flight begins, a distinct possibility since all these species rapidly warm above the takeoff temperature if forced to "fly" while suspended by one wing.

Examination of the relationship of warm-up rate to T_a permits an analysis of the energetics of warm-up. Heinrich and his coworkers (Heinrich and Bartholomew, 1971; Heinrich and Casey, 1973; Bartholomew and Casey, 1973) showed in moths that warm-up rate increases markedly with increasing T_a. They concluded that heat production during warm-up is determined by T_b and is not varied in direct response to ambient conditions. Among dragonflies warm-up rate increases with T_a in *Miathyria*, *Tramea*, and *Macromia*. In *Anax*, however, the picture is very different. In males the warm-up rate is nearly constant at T_a from 15°C to 25°C, and in both sexes it declines from 25°C to 30°C ($0.90 < p < 0.95$ in males, $0.95 < p < 0.975$ in females). Since recording was continuous and chart speeds of about 0.25 cm/min were used, I do not think that serious error exists in determining these rates.

The results in *Anax* clearly are not compatible with the idea that heat production is independent of T_a, so I compared calculated heat production of all species at various T_a. Since

$$\text{heat production} = \text{heat storage} + \text{heat loss},$$

$$\text{heat production} = \text{warm up rate} \times \text{specific heat} + C(T_b - T_a).$$

During warm-up abdominal temperatures sometimes rise faster and to a higher level at high T_a than at low T_a. This difference indicates more circulation between thorax and abdomen at high T_a during warm-up as well as during cooling. Therefore, values of C calculated from the data in Table 10 were used in calculating heat loss. This method minimizes apparent differences in heat production.

The results of these calculations appear in Table 10. They show that heat production decreases as T_a increases in *Anax*, particularly in males. The values also indicate a decline in heat production in *Tramea* and perhaps in *Macromia*. Even though the warm-up rate of these species increases with T_a, it does not do so as fast as if maximal metabolic rates were maintained. *Miathyria* was not included in this comparison because their brief warm-up seriously reduced the accuracy of determinations of rates. Measures of dispersion are not indicated since these values are the result of operations on several quantities for which data of variable precision are available, and the dispersion of the final results may not accurately reflect their uncertainty. However, the consistent trends toward lower rates of heat production at progressively higher T_a suggest that the results are valid.

Heinrich and Bartholomew (1971) draw attention to the effects on warm-up rate of heat loss due to evaporation and forced convection caused by wing movements. If either of these factors varies significantly with T_a it could affect the results of Table 10. At a given T_b convective heat loss should be higher at lower T_a because it depends on T_b - T_a, so this cannot explain apparently higher heat production at

Table 10. Heat prodution during warm-up in Odonata.

Species	T_a (°C)	Mean Weight Thorax (g)	Mean Warm-up Rate (°C/min)	Mean T_b at takeoff (°C)	Heat Production (cal/g·min) at indicated T_b				
					15°C	20°C	25°C	30°C	Takeoff
Anax junius ♂	15	0.427	3.85	33.4	3.16	4.10	5.05	5.99	6.64
	20	0.419	4.39	34.6		3.60	4.63	5.65	6.60
	25	0.444	4.22	36.7			3.47	4.65	7.25
	30	0.468	3.10	35.8				2.55	3.88
Anax junius ♀	15	0.427	3.20	37.0	2.62	3.56	4.51	5.45	6.77
	20	0.409	5.34	36.1		4.38	5.41	6.43	7.68
	25	0.417	6.07	37.9			4.96	5.44	8.03
	30	0.422	4.20	38.0				3.44	5.28
Macromia taeniolata	15	0.591	1.91	37.4	1.56	2.30	3.04	3.78	4.87
	20	0.640	2.56	35.0		2.10	2.92	3.74	4.56
	25	0.618	3.43	33.5			2.59	3.37	3.91
	30	0.562	4.26	34.1				3.49	4.23
Tramea carolina	15	0.160	1.72	30.8	1.37	2.56	3.75	4.93	5.13
	20	0.164	2.30	28.2		1.89	3.16	--	3.97
	25	0.172	3.00	33.6			2.44	3.75	4.70
	30	0.145	4.19	34.5				3.44	4.69
Miathyria marcella	25	0.077	2.72	27.1			2.23	--	3.09

low T_a. Evaporation depends on T_b and the saturation deficit of the surrounding air. Humidity was uncontrolled in these experiments, so the saturation deficit was undoubtedly higher at high T_a, resulting in increased evaporative water loss and perhaps in a reduction in heating rate. To test this possibility two additional sets of warm-up experiments on *Anax* were run at 25°C. In one group each insect was placed in a desiccator over silica gel, so that relative humidity was near 0%. In the other group, each individual was run in a desiccator over distilled water so relative humidity was about 100%. The results (Table 11) show that humidity does not affect warm-up rate significantly. In both groups T_b at takeoff was somewhat lower than in individuals at ambient relative humidity, but this may have been due to the small space in which they were confined.

Although heat production was not maximal, Figure 39 shows that duration of warm up decreases rapidly with increasing T_a, so the period of greatest exposure to potential predators is greatly reduced. Although the duration could be reduced further, it probably represents a compromise between minimizing exposure and the cost of warming.

Table 9 shows that species that warm up endothermically are fliers or, if perchers, are large. Parameters relating to warm-up show rather interesting correlations with body size. For example, Figure 40 shows that in *Tramea*, T_b at takeoff increases with increasing body weight. In *Miathyria*, takeoff T_b shows no relationship with body weight, but it is close to values expected from *Tramea* at the same body weight. In *Anax*, T_b at takeoff increases with weight up to a point, then levels off (Figure 41). No apparent correlation occurs in *Macromia*, but the range of body weight is small (Figure 41).

Table 11. Effect of humidity on warm-up in *Anax junius* at T_a = 25°C.

R.H.	Mean warm-up rate ± S.D. (°C/min)	N	Mean T_b at take off ± S.D. (°C)	N
0	6.08 ± 0.47	6	35.6 ± 1.59	5
100	6.12 ± 1.56	5	36.4 ± 2.06	4

Figure 39. Duration of warm-up as a function of T_a in several species of dragonflies. Time was calculated from the mean warm-up rate and T_b at takeoff for each group. The dotted line indicates the duration calculated for male *Anax junius* if heat production were maximal at all T_a. Symbols are as follows: Δ - *Macromia taeniolata*, □ - *Tramea carolina*, ○ - *Anax junius* female, • - *Anax junius* male.

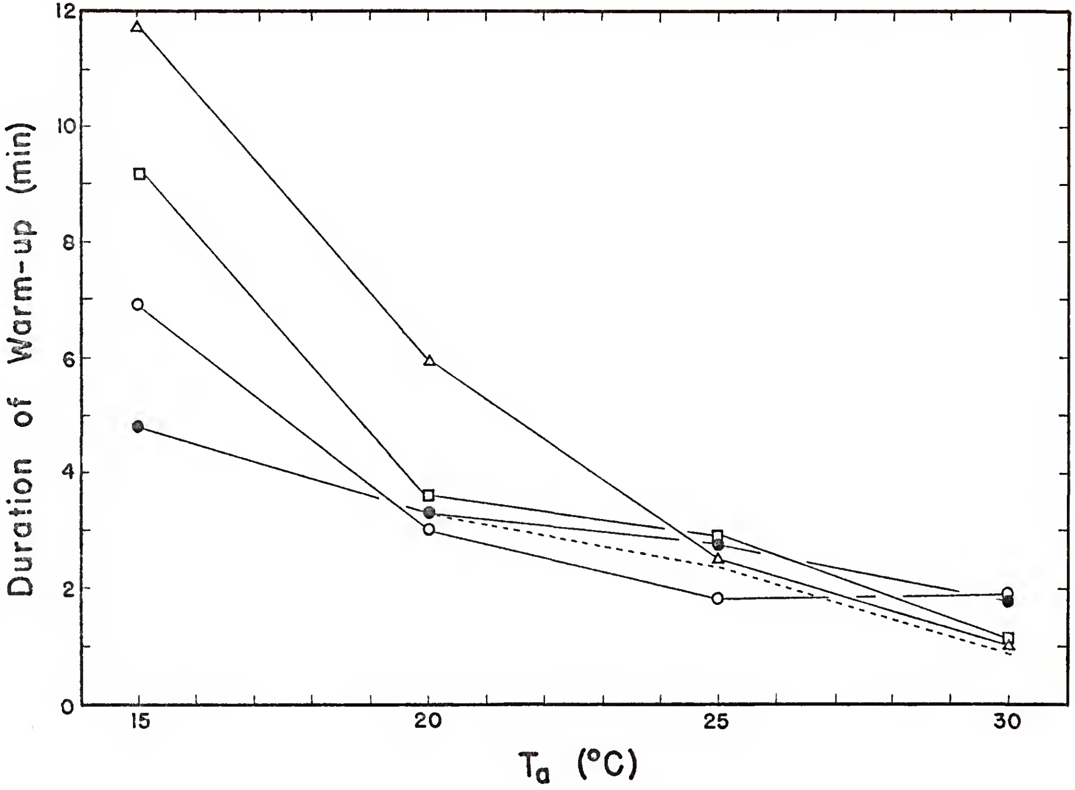

Duration of Warm-up (min)
0
2
4
6
8
10
12
T_a (°C)
15
20
25
30

Figure 40. T_b at initiation of flight as a function of body weight in *Tramea carolina* and *Miathyria marcella*. The lines were drawn by eye. Symbols are as follows: ∘ - *Tramea* at 20°C, ▲ - *Tramea* at 25°C, △ - *Tramea* at 30°C; □ - *Miathyria* at 25°C.

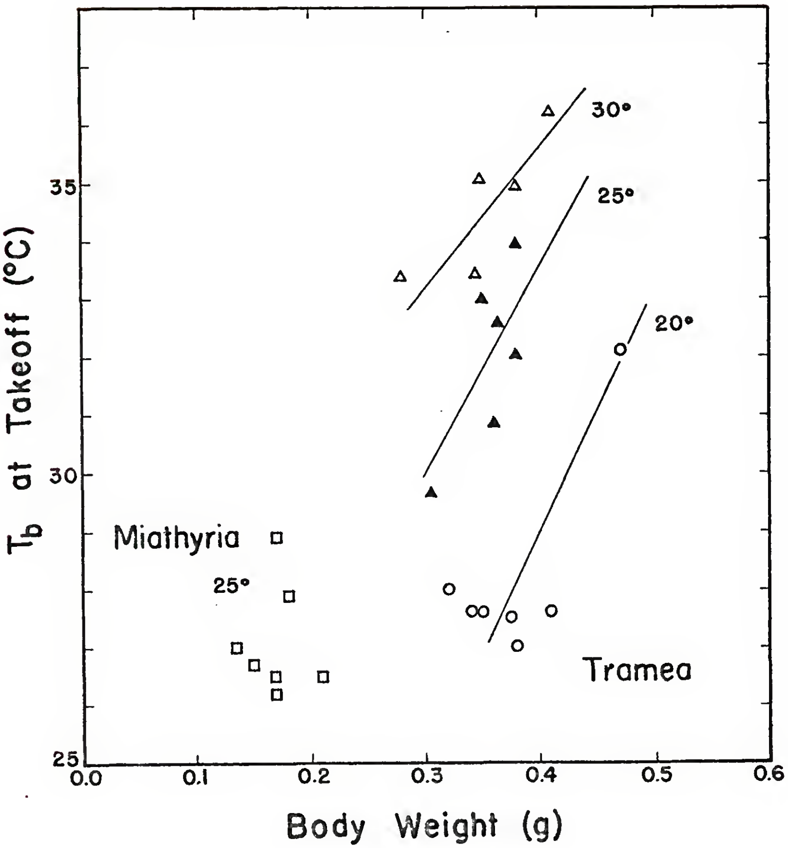
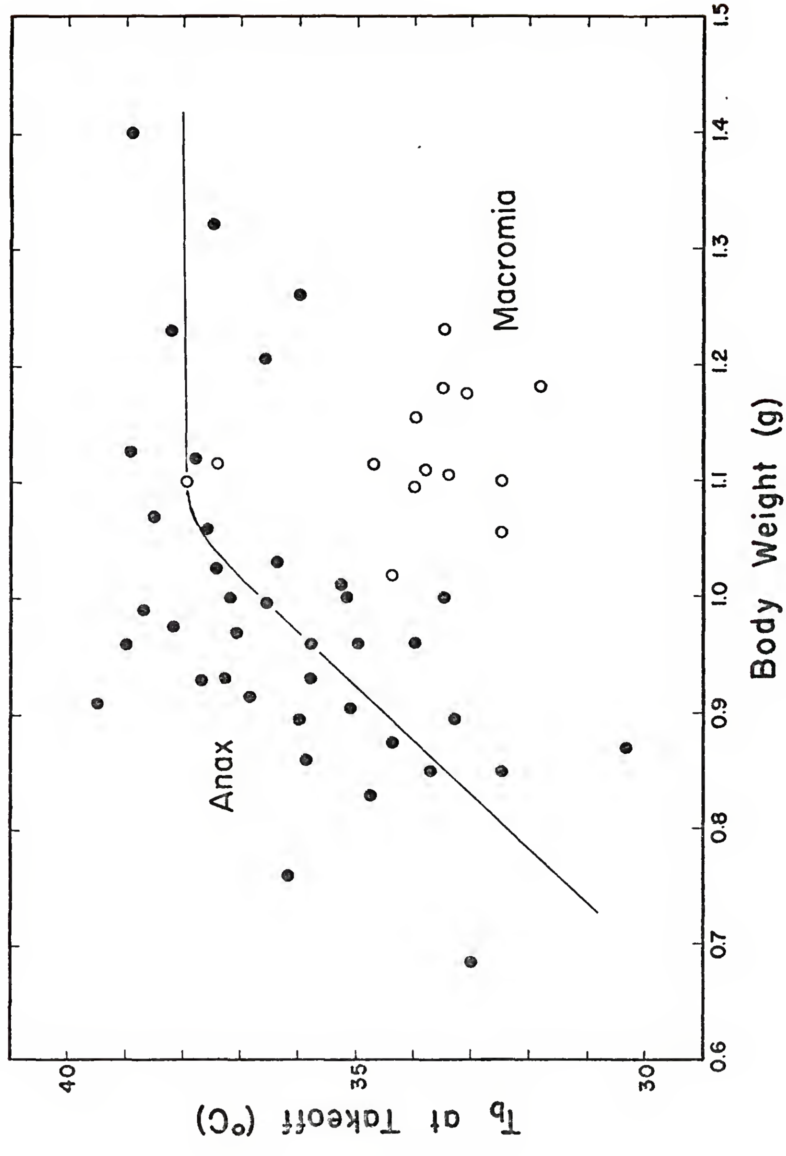

30°
25°
20°
Miathyria
25°
Tramea
T_b at Takeoff (°C)
Body Weight (g)
25
30
35
0.0
0.1
0.2
0.3
0.4
0.5
0.6

Figure 41. T_b at initiation of flight as a function of body weight in *Anax junius* (•) and *Macromia* (○). The line was drawn by eye through the data for *Anax*.


T_b at Takeoff (°C)
40
35
30
Body Weight (g)
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
1.5
Anax
Macromia

These results bear a striking resemblance to those of Bartholomew and Heinrich (1973) relating T_b in moths in free flight to body weight and wing loading. They argued that body weight *per se* above 0.1 g is not important in determining T_b, but that wing loading (the ratio of wing area to body weight) is. An insect with small wings relative to its weight must work harder to generate adequate lift. A related principal may be operating here. Since the power input (*i.e.*, metabolism) that insects generate is a function of T_b (Neville and Weis-Fogh, 1963) and since lift required to take off relates to wing loading (Dorsett, 1962), one might expect dragonflies with high wing loading to take off at higher T_b than those with low wing loading. I have not measured wing loading, but within a species and it should increase with body weight, since surface area generally is a function of $W^{2/3}$. Therefore T_b at takeoff should increase with body weight, and this occurs. Variations among different species in the relation of wing loading to body weight and of power input to temperature complicate the relationship of takeoff temperature and body weight.

A similar hypothesis may explain why female *Anax* have slightly higher body temperatures than males at low T_a in the field. The former are generally heavier (Table 4) but have a relatively smaller thorax. Thus wing loading is probably higher in females and they may therefore require a higher T_b for efficient flight. Gravid female sphingids often takeoff at higher T_b than males (Dorsett, 1962).

Heinrich and Bartholomew (1971) examined the correlation between body weight and warm-up rate in heterothermic birds and mammals and in insects. They concluded that warm-up rate generally decreases with increasing body weight. However, their data show that among insects warm-up rate is independent of, or even increases slightly with, body weight. Among different species of dragonflies a definite increase in rate occurs with greater size, at least up to a thoracic weight of 0.5 g (Figure 42). The same trend is evident within *Tramea* and possibly in *Miathyria* (Figure 43), although in the latter the uncertainty of each rate determination is high. In *Anax* and *Macromia* no evident correlation of rate with thoracic weight exists. Thoracic weight is the most appropriate measure of size in insects, since heat production is confined to the thorax. In insects warm-up rate apparently is not related to body size in the same way as in vertebrate heterotherms.

The difference between insects and vertebrates may be rationalized as follows. The analysis is much simplified by partially ignoring the effect of changing temperature on heat production and loss and by assuming that in mammals and birds arousing from torpor, as well as in insects, T_b increases linearly with time. While this assumption is inaccurate in many cases (Hudson, 1973), it is convenient.

During warm-up, at any given time

heat storage rate = heat production rate - heat loss rate

$$RWk = M - C'(T_b - T_a)W$$

where R = warm-up rate (°C/min), W = thoracic weight of insects or body weight of vertebrates (g), k = specific heat of tissue (cal/g·°C), M = metabolic rate (cal/min), and C' is thermal conductance (cal/g·°C·min). Assuming that the usual power functions of weight describe M and C', and arbitrarily letting $T_b - T_a = 10°C$, which is reasonable if $T_a = 25°C$, as in Heinrich and Bartholomew's analysis, then

Figure 42. Warm-up rate as a function of thoracic weight in various species of Anisoptera at T_a = 25°C. Symbols as in Figure 36. Open circles represent single determinations. Species are: a - *Miathyria marcella*, b - *Tramea carolina*, c - *Gynacantha nervosa*, d - *Nasiaeschna pentacantha*, e - *Gynacantha tibiata*, f - *Epicordulia regina*, g - *Coryphaeschna perrensi*, h - *Anax junius* male, i - *Anax junius* female, j - *Coryphaeschna ingens*, k - *Macromia taeniolata*.

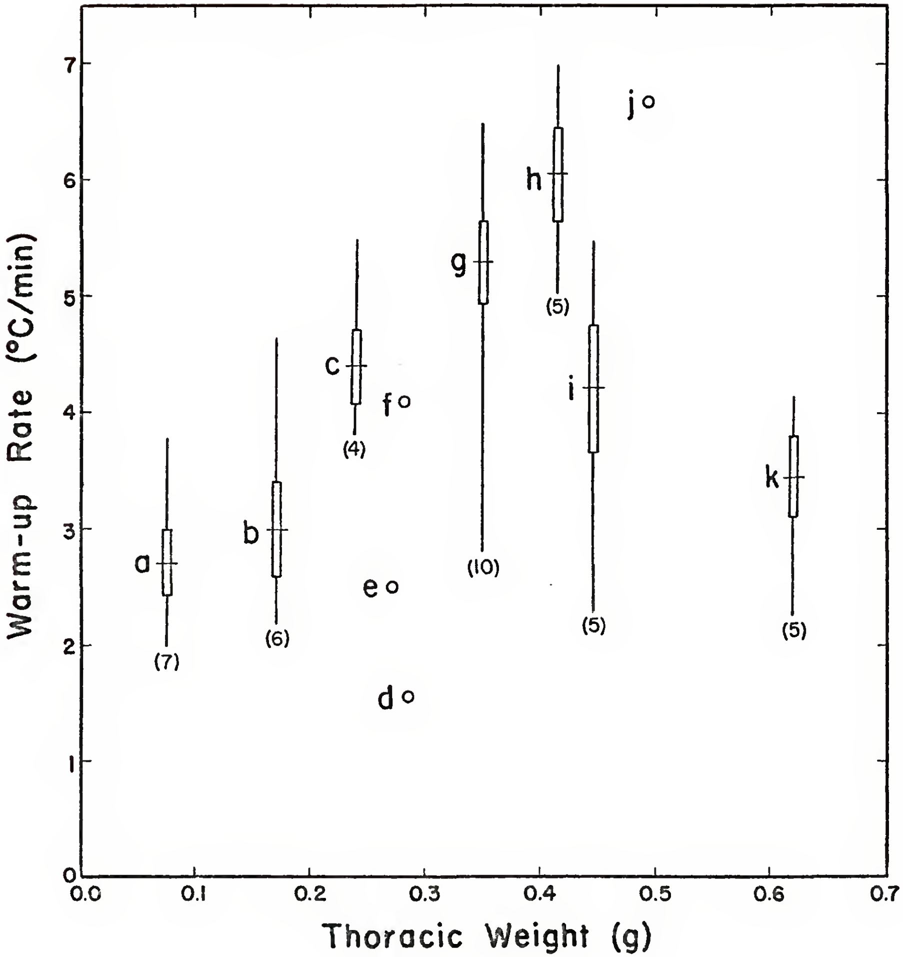
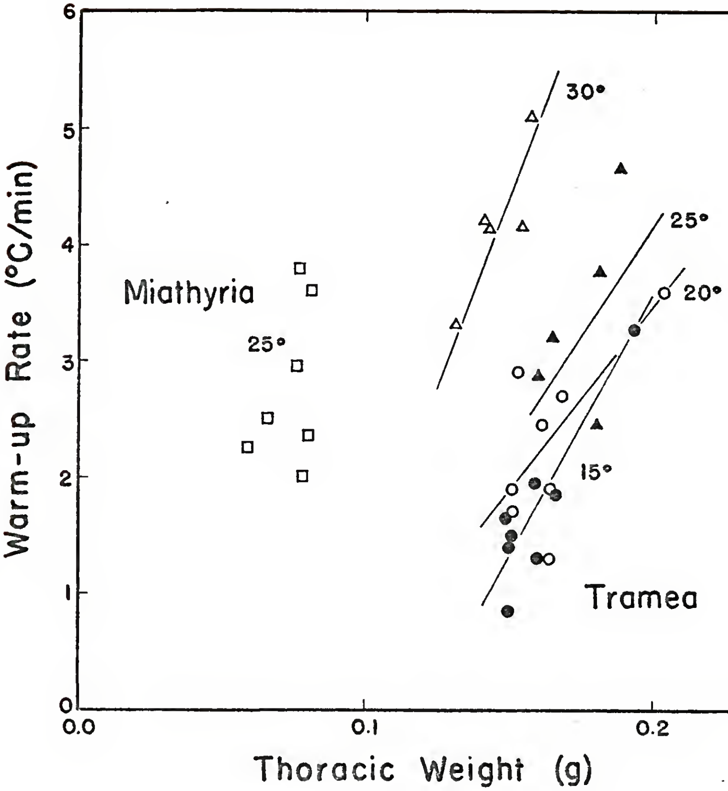

Warm-up Rate (°C/min)
Thoracic Weight (g)
0
1
2
3
4
5
6
7
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
a
(7)
b
(6)
c
(4)
d
e
f
g
(10)
h
(5)
i
(5)
j
k
(5)

Figure 43. Warm-up rate as a function of thoracic weight in *Tramea carolina* and *Miathyria marcella*. Lines were drawn by eye. Symbols as in Figure 40, • - *Tramea* at T_a = 15°C.


Warm-up Rate (°C/min)
Thoracic Weight (g)
0
1
2
3
4
5
6
0.0
0.1
0.2
Miathyria
25°
30°
25°
20°
15°
Tramea

$$0.82\ RW = aW^{b} - 10\ mW^{n}W$$

$$R = a'W^{b\,-\,1} - 10\ m'W^{n}. \qquad (1)$$

If one assumes that in mammals: 1) the maximal metabolic rate during arousal from torpor has the same relation to weight as does basal metabolic rate, *i.e.* $M \propto W^{0.75}$, but is about six times higher (the coefficient is based on data from Hudson, 1973, and Hammel *et al.*, 1968); and 2) C' follows the Herreid and Kessel relation, equation (1) becomes

$$R = 2W^{-0.25} - W^{-0.5}. \qquad (2)$$

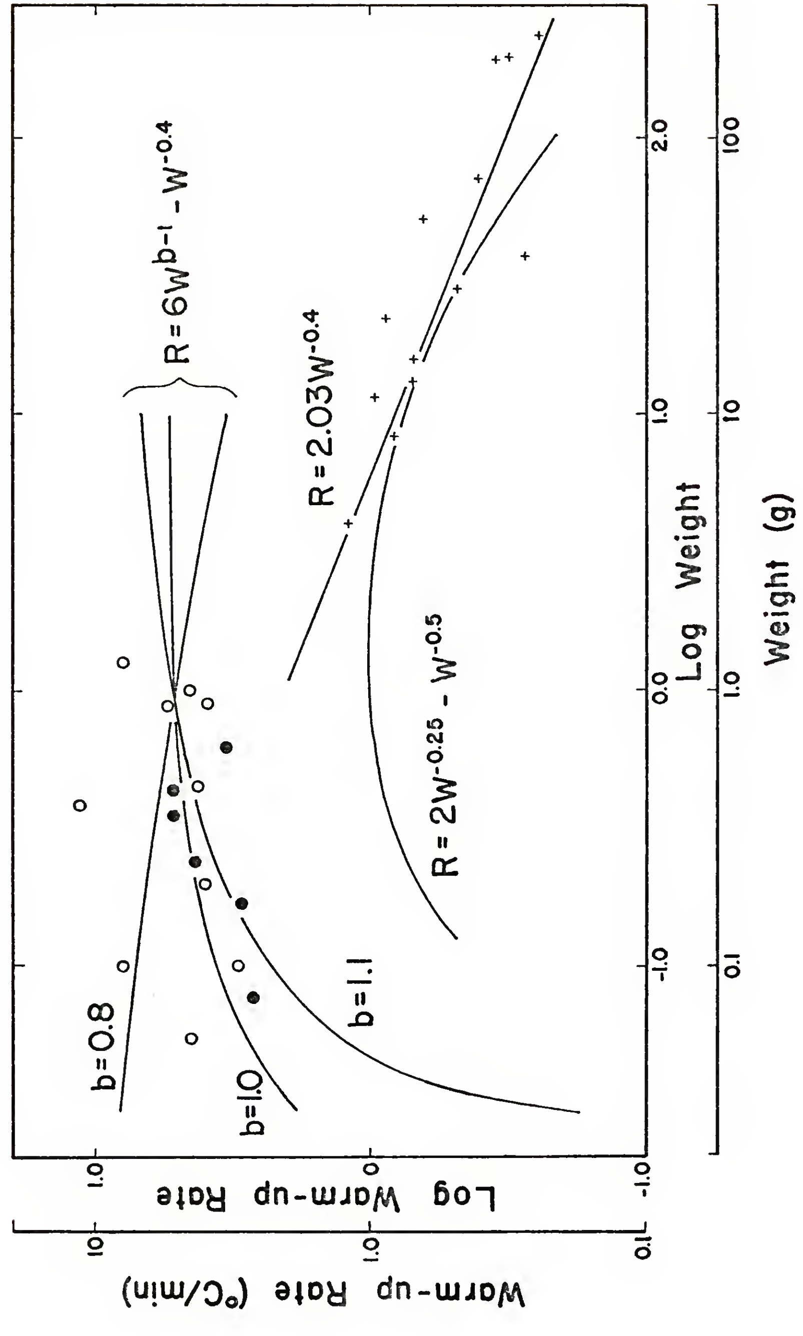
Equation (2) is compared in Figure 44 to the data on warm-up vs. body weight in mammals and birds from Heinrich and Bartholomew. The agreement is close considering the many simplifications.

The relationship of metabolic rate and conductance to body weight is poorly known in insects. Assuming that conductance generally follows the equations for live dragonflies and that a' is about 6, based on Table 10 and data from Heinrich and Bartholomew on *Manduca sexta*, then

$$R = 6W^{b\,-\,1} - W^{-0.4}. \qquad (3)$$

There is no generally accepted value for b in insects, even for resting metabolism. Based on few data but a wide weight range, Enger and Savalov (1985) give a value of about 0.8 for nonflying cockroaches and phasmids. Keister and Buck (1964) cite considerable evidence for a value near 1.0. The data in Table 10 suggest that in active dragonflies the value may actually be greater than 1.0. Figure 44 shows several possible relations of R to W, based on different values of b, as well as actual values for a number of insects. If b is between

Figure 44. Theoretical relationship between warm-up rate and weight in mammals and insects. Data on dragonflies (•) from the present study, those on other insects (°) and mammals (+) from Heinrich and Bartholomew (1971). The straight line log-log relation of rate to weight in mammals is also due to Heinrich and Bartholomew (1971). See text for derivation of other equations. Thoracic weights of insects from Heinrich and Bartholomew was assumed to be 50% of whole body weight.


R = 6W^{b-1} - W^{-0.4}
b=0.8
b=1.0
b=1.1
R = 2.03W^{-0.4}
R = 2W^{-0.25} - W^{-0.5}
Log Weight
-1.0
0.0
1.0
2.0
Weight (g)
0.1
1.0
10
100
Log Warm-up Rate
1.0
0
-1.0
Warm-up Rate (°C/min)
10.0
1.0
0.1

0.8 and 1.1, there is a reasonably good agreement between the rates of warm-up and those predicted by equation (3) from body size. This model accounts reasonably well for the data at hand. Both conductance and weight specific metabolism usually increase with decreasing size. Conductance increases more markedly, however, so that, at very small sizes, heat loss is so rapid that the higher metabolic rate is insufficient to fully compensate for the loss, and warm-up rate decreases. No mammals are sufficiently small for this to occur. Most insects, however, are so small that warm-up rate is independent or positively correlated with body size.

Critical Temperatures

Five levels of body temperature characterize thermal adaptations of flying insects: 1) the temperature at which cold torpor occurs, 2) the lowest temperature at which flight can be sustained, 3) the minimum voluntarily tolerated temperature, 4) the maximum voluntarily tolerated temperature, and 5) the temperature producing heat torpor. Neither the threshold of cold torpor nor minimum voluntary tolerance have been measured in the laboratory, although the latter may sometimes be inferred from field data. Data are available on the other parameters, and their relation to temperatures recorded in the field appears for each species on the respective plots of T_b vs. T_a

Minimum Temperature for Level Flight

The level of the lowest T_b at which flight can be sustained is vitally important to dragonflies. Some insects carry on a variety of activities even if they cannot fly. At temperatures below the minimum for flight cicadas feed (Heath *et al.*, 1972) and may be able mate and oviposit (Heath, 1967). However, essentially all activities of dragonflies depend upon attaining a T_b that permits flight.

In all species, body temperatures recorded in the field were generally well above mean minimum flight temperature. Even during the coolest hours before dawn, the body temperatures of active dragonflies were always above the minimal temperature for flight. In all cases in which perchers were active before dawn, T_a was above minimum flight temperatures. The smallest recorded excess of T_b over minimum flight temperature was a *Pachydiplax* at T_b = 22.0°C just after sunrise (T_a = 16.0°C). Most species were active at T_a's below the lowest T_b at which they can fly, so they must raise T_b before beginning normal activities, either by basking or by wing-whirring.

Two sorts of attributes probably determine minimum flight temperature in any insect. First, it must depend on the amount of lift and thrust per unit weight that can be generated for a given power input. Lift is inversely related to wing loading, which depends partly on how much the insect carries in the form of egg masses, viscera, and other dead weight. Second, biochemical and biophysical properties of the muscle fibers, especially their temperature dependence, will obviously influence the ability to fly at a given T_b. Neville and Weis-Fogh (1963) showed that in desert locust flight muscle, twitch duration decreases rapidly with increasing temperature from 25° - 40°C. They calculated that below the minimum flight temperature in locusts, more than 30% of the work done during maximum muscle activity is wasted because contractions of antagonistic muscles overlap. The same thing is probably qualitatively true of other insects.

Wing loading is determined largely by morphology, and, while it is certainly subject to evolutionary adaptation within the limits of the basic dragonfly design, it is more or less fixed for a given species or closely related group of species. The second factor, however, is not only likely to be subject to fairly rapid evolutionary change, but also has much greater potential to respond directly by acclimation to varying environmental conditions.

Wing areas were not measured, so a direct comparison of wing loading is impossible. Wing loading probably increases with increasing body weight, especially when closely related, and thus similarly shaped, species are compared. Figure 45 and Table 12 summarize the results on minimum flight temperature. As expected, an overall increase in minimum flight T_b occurs with increasing body weight. Unfortunately, there are few data at weights between 0.5 and 1.0 g, and most of the small species are libellulids while the large species belong to other families. Some additional evidence indicates that size is an important factor. Figure 45 shows five pairs of species in which members of each pair are in the same or closely related genera and are from the same general locality but differ in size. In four of these, the heavier species has the higher minimum flight T_b. The exceptional pair, *Tauriphila argo* and *Tramea walkeri*, actually supports the hypothesis that wing loading is an important determinant of minimum flight temperature. *Tauriphila*, the smaller species, has the base of the hind wing considerably less expanded than *Tramea*, so the relative wing area is undoubtedly less. No apparent correlation between body weight and the lowest temperature of sustained flight occurs within any single species, perhaps because of the relatively small range of weight found within a species.

Figure 45. Minimum T_b for sustained flight as a function of body weight in Anisoptera. Mean values are indicated by closed circles in temperate zone species, open circles in tropical species. The vertical lines extend one standard error on each side of the mean. Oblique dashed lines connect pairs of related species. The species are: a - *Pachydiplax longipennis*, b - *Ladona deplanta*, c - *Erythemis simplicicollis*, d - *Triacanthagyna trifida*, e - *Libellula* spp., f - *Miathyria marcella*, g - *Tramea carolina*, h - *Orthemis ferruginea*, i - *Gynacantha nervosa*, j - *Nasiaeschna pentacantha*, k - *Anax junius*, l - *Epiaeschna heros*, m - *Macromia taeniolata*, n - *Micrathyria aequalis*, p - *Micrathyria ocellata*, q - *Erythemis credula*, r - *Erythemis plebeja*, s - *Tauriphila argo*, t - *Tramea walkeri*.

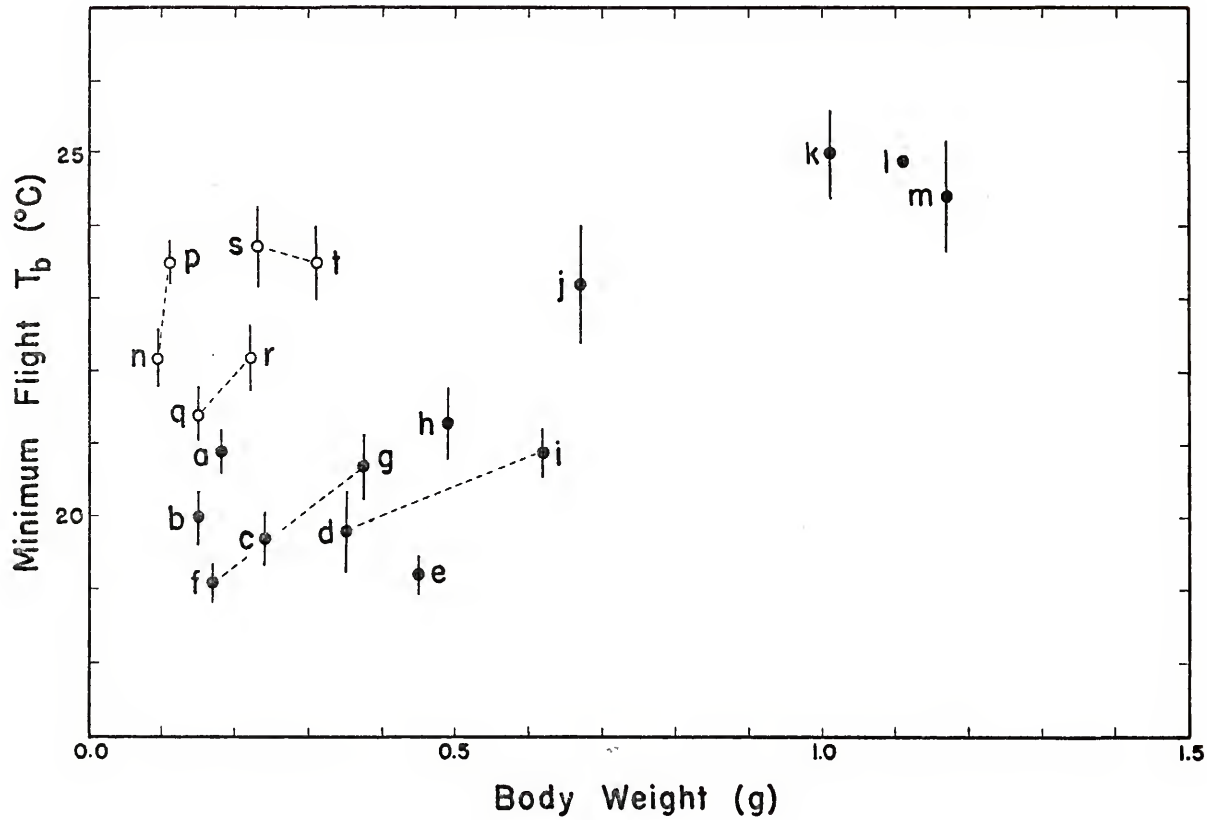

Minimum Flight T_b (°C)
25
20
Body Weight (g)
0.0
0.5
1.0
1.5
n
p
q
r
s
t
a
b
c
d
e
f
g
h
i
j
k
l
m

Table 12. Minimum T_b for sustained flight in Odonata.

Species	Sex	N	Mean Body Wt. (g)	Mean Min. Flt. Temp. + S.D. (°C)	p[a]
Anax junius	--	19	1.066	25.0 + 2.57	
	♂	8	1.041	23.9 + 2.68	0.90 - 0.95
	♀	11	1.085	25.8 + 2.27	
Epiaeschna heros	♂	1	1.110	24.9	
Erythemis credula	♂	10	0.153	21.4 + 1.16	0.90
E. plebeja	♂	10	0.212	22.2 + 1.44	> 0.995
E. simplicicollis	--	30	0.244	19.7 + 1.99	
	♂	15	0.214	19.5 + 1.74	0.70
	♀	15	0.274	19.9 + 2.26	
Gynacantha nervosa	♀		0.620	20.9 + 0.62	0.80 - 0.90
Triacanthagyna trifida	♂	8	0.348	19.8 + 1.54	
Ladona deplanata	♂	15	0.150	20.0 + 1.40	
Libellula spp.	--	29	0.449	19.2 + 1.40	
	♂	10	0.434	19.6 + 1.22	0.85 - 0.90
	♀	19	0.457	19.0 + 1.47	
Macromia taeniolata	♂	10	1.173	24.4 + 2.35	
Micrathyria aequalis	--	7	0.096	22.2 + 1.01	> 0.99
M. ocellata	♂	10	0.111	23.5 + 0.86	
Nasiaeschna pentacantha	♂	2	0.668	23.2	
Orthemis ferruginea	--	9	0.489	21.3 + 1.47	
Pachydiplax longipennis	--	41	0.176	20.9 + 1.91	
	♂	26	0.180	20.7 + 1.86	0.75 - 0.80
	♀	15	0.170	21.2 + 2.00	
b	--	10	0.173	19.6 + 1.27	0.99
c	--	31	0.177	21.2 + 1.94	

Table 12 Continued

Species	Sex	N	Mean Body Wt. (g)	Mean Min. Flt. Temp. ± S.D. (°C)	p^a
Miathyria marcella	--	20	0.174	19.1 ± 1.21]	0.97
Tramea carolina	--	20	0.374	20.7 ± 1.99]	
T. walkeri	♂	10	0.309	23.5 ± 1.63]	> 0.95
Tauriphila argo	--	10	0.234	23.7 ± 1.69]	0.55 - 0.60

---

[a] probability that the bracked pairs differ (one-tailed Student's t test).

[b] specimens collected in April.

[c] specimens collected July through October.

Table 12 shows four species in which enough individuals of both sexes were tested. Females require a higher T_b in order to fly in three of them. In *Pachydiplax* this trend occurs even though males are slightly heavier. In every case, females have a smaller thorax in proportion to body weight than males, no doubt due to their larger, often egg-filled abdomens. Since they evidently have higher wing loading and relatively less tissue involved in generating energy for flight, females probably must use their energy more efficiently and therefore require a higher T_b. *Libellula* spp. are exceptional in that males have a slightly higher minimum flight temperature. These species also seem to have a low minimum flight temperature for their weight.

Another major influence on minimum flight temperature is climate. Heath *et al.* (1971) found little variation in the minimum temperature for flight in cicadas over a range of elevation of about 2600 meters. However, among odonates, small and medium sized tropical libellulids require higher body temperatures to fly than do similar temperate zone species. The difference is especially striking in comparing temperate and tropical species in the same genus. In both *Erythemis* and *Tramea*, the Panamanian species have minimum flight temperatures significantly higher than the corresponding temperate zone species. Air temperature rarely falls below about 20°C in the Canal Zone, so there is much less selective pressure to develop the capability to fly at low T_a.

Additional support for the contention that minimum flight temperature is adapted to the thermal environment is supplied by data on *Pachydiplax*. Specimens taken in April could fly at a substantially lower T_b than those from July-October. Some seasonal variation in size in *Pachydiplax* has been reported (Penn, 1951), but it is not reflected in this sample. Other species were tested over a shorter period of time.

Limits of Voluntarily Tolerated Temperature and Temperature of Heat Torpor

The maximum and minimum levels of voluntary tolerance may be interpreted in light of the "dual set point" theory of temperature response in poikilotherms, outlined by Heath (*e.g.* Heath, 1967, 1968; Hanegan and Heath, 1970c). According to this model, a heliotherm will bask until the temperature of some nervous center, or of some integrated system of peripheral and central receptors, exceeds a fixed level, the lower set point. If the animal abandoned its basking posture immediately its temperature would again fall below the lower set point, so it is likely to remain in a position facilitating heat gain until it reaches a T_b equal to the upper set point. At this time the heliotherm stops basking until T_b falls below the lower set point. If T_b rises above the upper set point, the individual adopts a posture that reduces further heating.

This model agrees with the observation that dragonflies often bask at high T_b. It is also consistent with the fact that heat avoidance postures are closely correlated with T_b, but postures that augment heating are better correlated with T_a (Figure 18A, B) especially in good thermoregulators like *Libellula*. Behavior that increases heating will be maintained over a wide range of T_b, as already noted, and in good regulators T_b will usually remain in the optimal range. This behavior will be especially associated with low T_a, since T_b is more likely to fall below the lower set point at low than at high T_a. Thus, the probability of capturing a basking insect is greater at low T_a.

Behavioral changes of heliothermic odonates permit estimates of upper and lower limits of voluntary tolerance from field data. However, a dragonfly in the field is carrying on many types of behavior more or less independent of T_b. These may require alterations in posture or degree of activity which in turn alter T_b and apparent levels of thermal preferenda. Therefore, field data must be interpreted with caution (DeWitt, 1967).

In *Pachydiplax* the upper limit of voluntary tolerance is probably between 37°C, the lowest T_b of specimens in the obelisk, and about 40°C, the highest T_b at which basking postures appear. The lower figure correlates well with the mean value found in laboratory studies (Table 13). Many specimens in the laboratory assume the obelisk at lower body temperatures than any recorded in the field (as low as 36.0°C). The reason is two-fold. As noted above, many factors other than T_b may influence posture in the field. Also, in the laboratory T_b was recorded at the moment that heat avoidance behavior was fully developed. In the field most specimens in the obelisk had been in this posture for some time, and T_b may have continued to rise. The minimum voluntarily tolerated temperature in *Pachydiplax* is probably about 31°C-33°C, as this is the range in which non-basking postures become common.

The mean T_b producing heat torpor in *Pachydiplax* in the laboratory is several degrees above the maximum T_b recorded in the field, so

Table 13. Maximum voluntary tolerance and threshold of heat torpor in Odonata.

Species	Sex	MVT ± S.D. (°C)	N	p[a]	HT ± S.D. (°C)	N	p[a]
Anax junius[b]	--	37.8 ± 1.54	10		45.6 ± 0.98	10	
	♂	37.3 ± 1.80	5	0.80 - 0.85	44.9 ± 0.90	5	> 0.995
	♀	38.3 ± 1.13	5		46.2 ± 0.50	5	
Epigomphus quadracies	♂	32.5 ± 0.71	3		---		
Erythemis credula	♂	39.3 ± 2.19	12		45.3 ± 2.01	11	
E. plebeja	♂	39.4 ± 1.91	11		46.0 ± 2.30	11	
E. simplicicollis	--	40.2 ± 2.16	24		46.5 ± 2.09	22	
	♂	39.6 ± 2.43	12	0.85 - 0.90	47.3 ± 1.59	12	0.97 - 0.99
	♀	40.7 ± 1.61	11		45.4 ± 2.27	9	
[c]	--	38.4 ± 2.25	8	> 0.995	45.1 ± 2.39	8	0.97 - 0.99
[d]	--	41.1 ± 1.19	16		47.2 ± 1.30	14	
Gomphus cavillaris	♂	35.2	1		---		
G. minutus	♀	39.5	1		---		
G. pallidus	♂	41.1	1		---		
Libellula spp.	--	39.2 ± 1.19	20		46.0 ± 1.06	20	
	♂	39.4 ± 1.00	10	0.75 - 0.80	46.3 ± 1.27	10	0.85 - 0.90
	♀	38.9 ± 1.58	10		45.7 ± 0.75	10	
Macromia taeniolata[b]	♂	36.2 ± 1.62	8		44.8 ± 1.01	8	
Miathyria marcella	--	42.6 ± 1.21	17		47.0 ± 1.07	16	
Micrathyria aequalis	--	37.7 ± 1.98	13		45.4 ± 1.59	13	
M. eximia	--	37.9 ± 2.25	6		44.7 ± 2.14	6	
M. ocellata	--	37.3 ± 2.76	15		44.4 ± 0.88	14	

Table 13 Continued

Species		Sex	MVT ± S.D. (°C)	N	p[a]	HT ± S.D. (°C)	N	p[a]
Pachydiplax longipennis		--	37.5 ± 2.12	54		45.5 ± 1.67	49	
		♂	37.7 ± 2.12	39	0.85 - 0.90	45.5 ± 1.51	36	
		♀	37.0 ± 2.12	15		45.4 ± 2.12	13	
	e	--	36.9 ± 2.00	28	> 0.996	44.9 ± 1.64	25	0.97 - 0.99
	f	--	38.2 ± 1.97	12		46.2 ± 1.45	11	
	g	--	38.3 ± 2.22	14		46.0 ± 2.21	13	
	f, g	♂	38.7 ± 1.57	18	0.975	46.2 ± 1.52	16	
	f, g	♀	37.0 ± 2.48	9		45.8 ± 2.51	8	
Tauriphila argo		--	42.1 ± 1.67	5		48.0 ± 1.58	5	
Tramea carolina		--	38.5 ± 1.85	11		46.8 ± 1.48	16	
T. cophysa and *T. walkeri*		--	39.0 ± 1.05	16		45.9 ± 1.20	6	

[a] probability that bracketed pairs differ (one-tailed Student's t test).

[b] values for these species of doubtful significance; see text.

[c] specimens collected in April and May.

[d] specimens collected June through September.

[e] specimens collected in May

[f] specimens collected in July and August]

[g] specimens collected October through December] grouped in comparing with specimens collected in May

individuals have some leeway before approaching dangerous thermal stress. The temperature at which acute heat exposure causes paralysis is probably the functional upper lethal temperature in the field, due either to further heating or exposure to predation while incapacitated.

Upper and lower voluntary limits in *Erythemis simplicicollis* were more difficult to recognize because no postures were identified as characterizing individuals within the preferred range of T_b. The upper limit may be about 40°C, since few specimens at higher T_b were in basking postures, and the highest T_b recorded in an individual perched on the ground was 40.8°C. This range agrees well with laboratory data. The lower limit is evidently below 36°C since individuals facing the sun are common at higher body temperatures.

Figure 18C gives the best indication of voluntary limits of *Libellula* spp. Most individuals are on the shaded side of stems at T_b above 38°C, agreeing well with the mean maximum voluntarily tolerated temperature found in the laboratory, 39.2°C. The minimum level of voluntary tolerance may be around 34°C, as specimens on the sunny side of stems exceed those in intermediate positions at this temperature.

Erythemis simplicicollis has a high heat torpor threshold and thus has as high a safety margin as *Pachydiplax*, despite its hotter microhabitat. *Libellula* spp. have a greater margin of safety because of their better T_b regulation.

Fliers do not show clear behavioral changes in response to temperature, so limits of tolerance are not available from field observations. The laboratory results show some interesting features, however. Both tropical and temperate zone species of *Tramea* have upper limits of voluntary tolerance similar to other libellulids, and heat torpor occurs at similar or slightly higher temperatures. *Miathyria* and *Tauriphila*, by contrast, show remarkably high voluntary tolerance and *Tauriphila* is also extraordinarily resistant to heat torpor. In the field neither species exceeded their limit of voluntary tolerance.

Although the smaller fliers tend to have lower eccritic temperatures than *Tramea*, they risk acute exposure to high T_b because their small size and consequently low rate of heat production and high thermal conductance limit their ability to thermoregulate. They may compensate for poor regulation by tolerating high body temperatures. One objection to measurements of the behavioral correlates of temperature is that neither *Tauriphila* nor *Miathyria* commonly perch, and the behavior patterns required to minimize heating under the test conditions may be poorly developed. However, neither species showed signs of agitation long before heat avoidance, and their behavior minimizing heating was not markedly different from other species.

Another problem arose in measuring voluntary tolerance in *Tramea carolina*. Some individuals began wing-whirring while being heated. Specimens that did this flew off the stick at a mean T_b of 35.2 ± 0.56°C (n = 5). Others hung quietly until moving away from the lamp at a T_b of 38.5 ± 1.85°C (n = 11). The difference is highly significant. Only the latter are included in Table 13.

All *Anax* wing-whirred while being heated and the mean avoidance temperature of males is lower than the T_b recorded in the field for most males during daylight. Only three of eight *Macromia* wing-whirred during heating, but the mean temperature at which avoidance was scored is below any value of T_b recorded in the field. Since *Macromia* can maintain a $T_b - T_a$ differential as low as 9°C, they should be able to remain below the apparent maximum voluntarily tolerated temperature at least up to $T_a = 27°C$. In both *Anax* and *Macromia* avoidance always was by flying off the stick.

Hanegan and Heath (1970c) proposed that elevation of the temperature of the thoracic ganglia above a critical level triggers initiation of flight and transition from warm-up to flight in *Hyalophora cecropia*. If a similar model applies to odonate fliers, the apparent avoidance level may actually represent the T_b triggering flight under the particular ambient conditions during heating. Comparison of Table 13 with Figures 36, 37, and 38A show that "avoidance" temperatures for *Anax*, *Macromia*, and wing-whirring *Tramea* correspond roughly to the transition from warm-up to flight at $T_a = 30°C$ in these species.

The mean temperature causing heat torpor is remarkably low relative to T_b recorded in the field in male *Anax* and especially in *Macromia*. Since these dragonflies are good regulators, perhaps they can afford to live close to their lethal limit. A more likely explanation is that thoracic core temperature is not the maximal body temperature of importance to these species when they are heated externally. McCrea and Heath (1971) reported that thermal sensitivity of *Celerio lineata* is not the same along the entire length of the nerve cord. Although circulation of blood may equalize temperatures somewhat, the temperature of the thoracic muscles must be substantially higher than other regions in large flying insects. Thus, the thorax may approach the level of heat torpor, but the actual sensitive region (perhaps the head) may remain well below the critical point.

It is also possible that the sensitive region was heated to a higher temperature than the thorax during investigations of heat torpor. However, in several cases the head was shaded during heating, with no marked effect on the threshold of torpor. Also, the insects usually struggled violently when heated above the maximum voluntarily tolerated T_b, so that if differences existed, thoracic core temperature was probably higher than other body temperatures.

Table 13 summarizes information on upper tolerance limits in many species. Few comparable data are available on other insects, but Heath and his coworkers have presented similar measurements from cicadas, moths, and katydids (Adams and Heath, 1964a; Heath and Josephson, 1970; Heath *et al.*, 1971). Their highest recorded values from a heliotherm were in the desert cicada, *Diceroprocta apache*, in which heat avoidance occurred at 39.2°C and heat torpor at 45.6°C. This insect inhabits an environment where air temperature regularly exceeds 40°C during the day. Air temperature is rarely above 35°C around Gainesville, yet heliothermic dragonflies from this region appear to be as heat tolerant as desert cicadas. No doubt the reason is that dragonflies remain largely exposed, both in flight and while perched, as long as they are active. *Diceroprocta* seeks shelter and flies sparingly during the hottest part of the day (Heath and Wilkin, 1970), although it continues to sing and presumably to mate. Some dragonflies may seek shade at midday (*e.g.*, *Tramea carolina* and *Macromia taeniolata*), but sexual and feeding behavior cease.

Both avoidance and heat torpor temperatures are adapted to the normal thermal environment of the insect. For example, all three species of *Erythemis* have higher limits of tolerance than other libellulid perchers. They all perch in the hot region on or near the ground, and the available data on *simplicicollis* and *plebeja* show higher body temperatures in the field than occur in species which usually select higher perches. *Epigomphus quadrices* is the only species studied that is normally restricted to deep forest, and it has a correspondingly low maximum level of voluntary tolerance.

Upper tolerance limits, unlike minimum flight temperature, are not notably higher in Panamanian species. During the spring and fall dragonflies may encounter considerably lower temperatures around Gainesville than ever occur in the Canal Zone, which accounts for the disparity in minimum flight temperature. Highest temperatures in Panama are seldom above 32°C whereas they regularly reach 33°C-35°C during the summer in Gainesville; consequently, no greater resistance to high temperature is required of the tropical species.

Heat avoidance and torpor also shows seasonal adaptation. *Pachydiplax* and *Erythemis simplicicollis* were tested at various times during the year. As Table 13 shows, both species voluntarily withstood higher temperatures in the summer and fall than in the spring, and *Erythemis* had a higher threshold of heat torpor in the summer. In *Pachydiplax*, specimens taken from October to December were similar to those from July and August and more heat resistant than those from May.

Heath *et al.* (1971) found that in cicadas both the maximum voluntarily tolerated temperature and the temperature producing heat torpor decrease with increasing altitude but the decline of the latter was much less. A single index to environmental temperature, such as altitude, could not be used to compare all these dragonflies, but the variation among species means is less for heat torpor than for the upper limit of voluntary tolerance. Within species, the standard deviation of the heat torpor threshold is less than that of maximum voluntary tolerance in twenty-one of twenty-nine cases in which both were measured (Table 13). Whether these differences are biologically significant is uncertain.

There is no apparent correlation between heat torpor or heat avoidance and body weight, either within or between species. There are significant sexual differences in avoidance and torpor temperatures in *Pachydiplax* and *Erythemis simplicicollis*. In *Pachydiplax*, the temperature resulting in torpor is about the same in both sexes, but maximum voluntarily tolerated temperature is higher in males, especially during summer and fall. This difference could be related to the necessity for prolonged exposure to high temperature during territorial defense. In *E. simplicicollis* the upper limit of voluntary tolerance is slightly higher in females, but heat torpor occurs at a lower temperature. This observation seems to hold regardless of season. I have no data on females of *E. plebeja*, but field observations indicate that they are generally adapted to lower temperatures than males (p. 61).

The standard deviations of maximum voluntary tolerance (as in Table 13) indicate the precision of active thermoregulation (Heath, 1965). The data from field studies are less satisfactory for this purpose because the behavioral responses may not be interspecifically comparable and in many cases the distributions of posture vs. temperature are far from normal. Few general trends are apparent from Table 13. There is no evident difference between tropical and temperate species in precision of heat avoidance responses. Among temperate perchers, *Libellula* spp. seem considerably more sensitive than *Erythemis* or *Pachydiplax*. Trameinae show less intraspecific variability in active response than do other libellulids (except *Libellula*), despite their more variable body temperatures in the field. Differences in precision of temperature responses of the on-off type shown in Table 13 are probably not the primary cause of differences in variability of T_b in the field. The adaptive significance of such differences in precision is therefore unclear. Alterations in posture in the field probably act as a proportional control on T_b (Heath, 1965) and may affect constancy of T_b more strongly.

CONCLUSIONS

It is now possible to summarize the principal responses of dragonflies to variable environmental temperature: 1) temperature conformity, 2) heliothermy, and 3) periodic endothermy. The three most important determinants of the type and success of the response are environment, body size, and behavior.

Conformers

Passive tolerance of the thermal environment is the simplest response to temperature, since it costs little time or energy; however, most organisms evidently function best within a fairly narrow range of body temperature. Unless the range of environmental temperatures to which an animal is exposed is narrow or the cost of regulation is very high, thermoregulation is advantageous.

The climate of the moist tropical lowlands is much more equable than that of temperate regions. This apparently reduces the necessity for thermoregulation in torpical dragonflies, although problems in interpreting the data for these species cloud the picture (p. 61). For instance, *Tramea* from Panama show no evidence of thermoregulation, while *Tramea carolina* definitely does. Several species of *Micrathyria*, all tropical perchers, show no evidence of regulation under most circumstances. These are small dragonflies, but in even smaller temperate zone species there are behavioral indications of temperature regulation.

Small size is another characteristic to be expected in conformers, however. Because small dragonflies have a very high conductance, their body temperature is closely coupled to air temperature. Even perchers, if small, are limited in their ability to use solar radiation for regulation (p. 201). Fliers have the additional problem of increased heat loss due to forced convection. Church (1960b) showed that forced convection is the primary avenue of heat loss in flying insects. Only the small flier, *Miathyria*, is a nearly exact conformer over a wide range of ambient temperatures. This species is also probably of tropical origin (Paulson, 1966). Even *Tramea carolina* regulates more poorly than the considerably smaller percher, *Pachydiplax*.

One adaptation that might be expected from conformers is a broad tolerated range, an expectation apparently realized in *Miathyria* and *Tauriphila*. Low minimum flight temperature also is associated with small size (Figure 45).

Heliotherms

Large insects probably cannot remain active throughout the day in exposed places without some form of thermoregulation. Black body temperatures often exceed 50°C during hot periods in both Florida and Panama. For long periods during cool weather air temperatures may be below the minimum temperature allowing flight. Behavioral control of thermal input opens up some otherwise unavailable niches. Such control requires a variable heat source, either regions of different temperatures within the habitat or a directional heat source like the sun. It also requires behavior that can be adapted to take advantage of such heat sources.

Among dragonflies, perchers are well suited for heliothermy. They remain stationary much of the time, so they are capable of selecting small areas of favorable thermal conditions and are able to control radiant heat load by fine postural adjustments.

Fliers, by contrast move through relatively large volumes of space and are less able to control their orientation toward the sun. None of the fliers, with the possible exception of *Macromia*, seem to alter their flight pattern to control solar heat load. Such behavior would be of little advantage to a flying dragonfly in any case. When heated only by an external source, its surface temperature must be higher than its core, especially since the subcuticular air sacs afford considerable peripheral insulation. To maintain a high core temperature, the surface to air temperature gradient must be quite steep. Since convective heat loss increases as this gradient increases, and since in fliers convection is forced, it is almost impossible to maintain a surface temperature much above air temperature, especially in small species. Perchers are less subject to forced convection and can selectively expose poorly insulated areas, such as the thoracic terga.

Body size is also an important factor in the thermal relations of heliothermic dragonflies. The sequence of perchers, *Pachydiplax*--*Erythemis*--*Libellula*, arranged in order of increasing body weight, shows a sequential decrease in the slope of T_b vs. T_a (Table 4).

The effects of body size on heliothermic reptiles have recently received some attention (Asplund, 1968; Bartholomew and Tucker, 1964; Hillman, 1969). Hillman (1969) found that three sympatric species of tropical lizards (*Ameiva*) maintained about the same T_b, but that the smallest species lived under a canopy transmitting the most sun and the largest under a canopy transmitting the least sun.

According to Porter and Gates (1969), the convection coefficient (k) of an object is proportional to $1/L^{2/3}$, where L is a linear dimension. Therefore, for convective heat exchange

$$dH/dt \propto k\ A$$

$$dH/dt \propto L^2/L^{2/3} = L^{4/3}$$

where A is surface area. In radiant heat exchange

$$dH/dt \propto \varepsilon\sigma A$$

where ε is emissivity and σ is the Stefan-Boltzman constant. Neither depend on the dimensions of the object, so

$$dH/dt \propto L^2$$

Thus, as size decreases the rate of convective heat exchange increases relative to the rate of radiant heat exchange. For this reason radiant heat input makes up a larger proportion of the total energy budget of large heliotherms than of small ones. This effect has two possible consequences. First, given equal solar exposure, large heliotherms will have higher T_b at equilibrium than small ones. Second, thermoregulatory ability may be enhanced in large organisms since alterations in radiant heat load, as by postural adjustments or shade seeking, have relatively greater effect on T_b.

These considerations apply only to equilibirum temperature. Total weight specific heat exchange is faster in small organisms. When environmental conditions fluctuate, large species will tend to have a more stable T_b but may sometimes have difficulty attaining a high T_b. However, all dragonflies are probably small enough to operate near equilibrium T_b under most circumstances

Little direct evidence exists for intraspecific effects of size on body temperature. Large *Pachydiplax* and *Libellula* have slightly higher temperatures at high T_a than do smaller conspecifics, and large *E. simplicicollis* may regulate a little better than small individuals (Table 4). Furthermore, large specimens of *Pachydiplax* bask less than small individuals (Table 14) but are found substantially more often in heat avoidance postures. Table 14 excludes one group of data, however, taken one early morning when most individuals were basking, at a site where almost all specimens were exceptionally large.

The presence in Panama of two black species of *Erythemis, E. plebeja* (mean body weight of males - 0.22 g) and *E. credula* (mean body weight of males - 0.15 g) made possible another test of the effect of body size on thermal relations. No data are available on free-ranging *E. credula* but Table 15 presents a tentative comparison of tethered specimens of the two species. All measurements were made on the same day using only mature males of both species. The larger species generally had a higher T_b when exposed to direct sunlight.

Several of the species that use the obelisk posture are of interest because of their small size (Table 6). *Perithemis tenera* and *Erythrodiplax connata* weigh about 0.05 g and *Nannothemis bella* is no more than half that weight. Even at this small size, postural adjustments are evidently effective despite the undoubtedly high convective heat loss, since the behavior has been retained.

Table 14. Distribution of postures according to weight class in *Pachydiplax*.

Weight Interval (g)	Mean Body Wt. (g)	N	% showing orientation indicated		
			Perpendicular	Not Perpendicular	Obelisk
≤ 0.15	0.126	49	32.6	49.0	18.4
0.15 - 0.20	0.173	43	32.5	39.5	27.0
≥ 0.20	0.226	18	11.1	50.0	38.9

Table 15. Relation of T_b to T_a in tethered specimens of black species of *Erythemis*.

			Shade		Sun	
Species	Mean T_a (°C)	Mean[a] Body Wt. (g)	Mean T_b + S.D. (°C)	N	Mean T_b + S.D. (°C)	N
Erythemis credula	29.8	0.153	32.8 ± 1.24	3	35.0 ± 2.10[b]	9
Erythemis plebeja	29.8	0.212	3.34 ± 0.91	3	36.0 ± 2.14[b]	9

[a] From Table 12.

[b] Probability that population mean for *E. credula* is less than that for *E. plebeja* is approximately 0.8 (one-tailed Student's t test).

Micro- and macroclimate are obviously important factors influencing thermoregulation in dragonflies. Tropical species such as *Erythemis plebeja* and *Micrathyria* spp. evidently do not regulate as well as similar temperate zone species. Also members of the genus *Erythemis* have high eccritic temperatures and high temperature tolerance as a result of their propensity to perch in the warm layer of air near the ground. This particular microenvironment may also facilitate regulation of T_b because it affords a relatively wide range of air temperature within a short vertical distance. On the other hand, variation in T_b may be increased by the great temporal variation of T_a near the ground.

Heath and Wilkin (1970) found that the desert cicada employs a boundary layer for thermoregulation. These cicadas perch in the cool layer on the shaded side of twigs during the heat of the day. They are near the upper limit of size permitting this behavior. In general, small insects that perch on broad surfaces will have more opportunities to take advantage of the special thermal conditions of boundary layers.

Endotherms

Well-developed endothermy can broaden still further the range of habitable thermal environments and is probably less costly than behavioral thermoregulation in terms of added exposure to predation and reduction in alternative activities. The energetic cost is enormous, however. Consideration of conductance and metabolic rate makes clear that a continuously resting insect cannot possibly regulate T_b endothermically (McNab, 1970). This avenue is open only when metabolism is tremendously increased during flight or, in special cases, other activities (Heath and Josephson, 1970). Insects can at best be only periodic endotherms.

Insect flight muscle is among the most active tissues known and a great deal of heat is produced as a by-product of its metabolism. The special adaptations required to use this energy source most effectively for temperature regulation, *e.g.*, low and variable conductance or heat production dependent on T_a, are likely to evolve only in species that spend most of their active period in flight. Insulating subcuticular air sacs probably first developed in fliers. The importance of this insulation in the development of endothermy in odonates is strikingly illustrated by the comparison of thermal conductances of dragonflies and mammals (Figure 34).

Perchers seem to be as well insulated as fliers, and they are capable of raising T_b during flight. However, the elevation of T_b during short periods of activity is slight, as discussed above. They probably have time to lose all of the endogenously produced heat during periods of perching. An exception to this rule may occur during periods of intense aggressive activity among males, but there is no evidence that this behavior is modified to maintain a relatively constant temperature. However, heliothermic dragonflies also benefit from the low thermal conductance, since heat retention is facilitated during cool periods when basking is possible only intermittently or when the sun is briefly obscured.

Body size is clearly important to thermoregulatory ability in fliers, perhaps more so than in perchers. The sequence *Miathyria* –

Tramea - *Anax* - *Macromia*, arranged in order of increasing size, shows progressively more constant T_b (Table 4). The same relation may hold among the tropical fliers, *Tauriphila* and *Tramea*. These field results in fliers are predictable from theoretical considerations and from laboratory studies. Conductance is a function of $W^{-0.3}$ to $W^{-0.5}$ (Figures 29-33), so

$$\text{heat loss (cal/min)} \propto W^{0.5} \text{ to } W^{0.7}.$$

Total heat production increases more rapidly with increasing weight, since

$$M(\text{cal/min}) \propto W^{0.8} \text{ to } W^{1.0}$$

(see p.176). This relation means that large fliers can maintain greater differences between T_b and T_a than small ones. This is important to thermoregulation regardless of the mechanisms by which T_b is adjusted. If evaporative cooling is of little importance, as seems reasonable (Table 11; Church, 1960a), and radiant heat loss to the sky is slight, T_b will be at least as high as T_a. Compare the situation of *Tramea carolina*, in which T_b = 32°C when T_a = 20°C; and *Macromia taeniolata*, which has T_b = 40°C when T_a = 20°C. If both are perfect regulators, *Tramea* could maintain T_b constant until T_a = 32°C, and above this point T_b would rise with T_a. *Macromia*, however, would be able to operate with unchanging T_b until T_a = 40°C. Conversely, if both species had the same optimum T_b, 40°C, *Tramea* could maintain this T_b only down to T_a = 28°C while *Macromia* could do so at least down to T_a = 20°C.

Small insects need not always be poorer thermoregulators than large ones. Bees as small as 0.1 g are good periodic endotherms

(Heinrich, 1972a, b, c, d). Preliminary results on *Tetragoneuria cynosura* (about 0.15 g) indicate that this species, about the size of *Miathyria*, controls T_b much better than the latter and probably better than *Tramea*. As McNab (1970) emphasized, thermoregulation is a complex process determined by the interaction of several variables, and good insulation or high metabolic rate can compensate for low body weight. *Tetragoneuria* probably has a high scope of heat production, since conductance is near the expected value for its weight (Figure 31).

The actual lower limit of size at which endothermy is possible depends on the maximum possible sustained metabolic rate, the length of the active period, and the energy reserves and intake of a particular insect. At the other end of the size scale, very large insects are almost obliged to develop mechanisms to maximize heat loss or else suffer restriction of activity because of overheating during flight. The latter apparently occurs in desert locusts since they often will not fly for more than a few minutes at high ambient temperatures (Church, 1960a).

The tropical species of *Tramea* do not regulate as well as *Tramea carolina*. Also, the tropical aeshnid subfamily, Gynacanthagyinae, are fliers, and they are endothermic in that they can warm-up by wing-whirring. The few data available indicate that they do not thermoregulate, however (personal observations). These facts suggest that the effects of climate on endothermic dragonflies are probably similar to those of heliotherms.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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